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Ecosystem theory and management[1]

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Introduction

In Western Australia, and particularly in the vicinity of Perth, man and his activities are producing a serious impact on the remaining natural ecosystems so that it is both prudent and desirable to intervene and manage them in order that further undesirable changes are avoided or reduced.

Adequate management of ecosystems requires a prescription for action which has a basis in a theory of how ecosystems function. However, ecosystems are naturally so complex that it is necessary to dissect them into component parts or processes for analysis. Thus study may be devoted to the chronological development of the ecosystem, or the diversity or complexity of the ecosystem, or competitive relationships within a community, or community structure (producer/consumer or predator/prey interactions). While these studies give insights into interactions, they throw little light on processes operating with communities which in turn are related to diversity, complexity and stability. These lie at the core of any understanding which can form the basis for management. Recent studies emphasise the structural components of ecosystems, e.g. species, while overlooking the other aspects of ecosystems, namely, the processes involved, especially their role or function, and it is this aspect that I propose to emphasise in the following brief development of a theory of how ecosystems might be integrated, and then apply the theory in a suggestive way to the local scene.

In order to construct a general theory I propose to take as a starting point the observation that life depends on the fixation of nitrogen and the elaboration of biologically complex molecules which can only be done by a limited variety of organisms. Once elaborated, these molecules are a resource to be exploited by organisms which cannot elaborate them. It is the pattern of elaboration and exploitation that constitutes the functional aspects of the ecosystem or community. That is, the construction of the theory relies on a biological approach which takes into account diversity, complexity and stability which earlier I suggested were near the core of understanding ecosystems.

Diversity

Taking the elaboration of biologically essential molecules as a starting point, it is possible to conceive or construct a hypothetical community in which the biological molecules enter the system by way of synthesisers and have a residual time in the community, which is related as an

$$\text{input}-\left\{\begin{matrix}\text{synthesis;}\\ \text{dinitrification}\\ \text{photosynthesis}\end{matrix}\right\}\longrightarrow\text{output}-\left\{\begin{matrix}\text{biological}\\ \text{degradation}\end{matrix}\right\}$$

system. The nitrogen fixed and the molecules synthesised are a resource to be exploited by organisms unable to synthesise them themselves. Without the interpolation of exploiting organisms a system could be conceived of as producers and degraders (bacterial decomposition). Without exploiting organisms the system is at its simplest when the most vigourous and actively reproducing and growing synthesiser outcompetes others for space and other resources. Diversity of producers will be increased when a fluctuating environment alternatively favours the fundamental niche (Hutchinson 1957) of one or the other of the synthesisers; or when exploiting organisms assume the role of predators of the synthesiser, the predators being favoured or not according to the way environmental changes exceed or otherwise the possible states of persistence defined by their fundamental niche; or when competitive interactions delimit the realised niche of some of the synthesisers or predators. By a combination of these interactions it is possible to go on packing the community with producers and consumers until the resources of space, nutrients, and biologically useful molecules can be divided no further and still support an exploiting population.

In this sense the variety of consuming organisms interpolated between the synthesisers and the degraders is a device for delaying the ultimate degradation of biological material by bacteria or increasing the residence time before ultimate degradation.

Complexity

The basis of the community is nitrogen fixation and the producers of biologically useful molecules, particularly amino acids and carbohydrates. The most easily measured of these basic entities are those concerned with trapped solar energy, that is, carbon flow. However, the flow of biologically useful nitrogenous compounds can be conceived as being of extreme importance since nitrogen is essential for growth and the nitrogen pool of the system could conceivably be more limiting than any ability to synthesise carbohydrates. The pool is of course replenished by nitrogen fixation, and in the Australian ecosystems there may be anaerobic prokaryotes, photosynthesising prokaryotes, lichens, rhizobial symbionts on legumes, or actinomycete symbionts on other plants, e.g *Casuarina*. Not all these routes of fixation operate all the

[1] Read at a seminar held at Murdoch University on 7 June 1980 as part of a series of meetings on the theme "Ecosystem management in Perth and its hinterland".

time: some are limited by seasonal conditions; others are limited by seral stages in plant succession, e.g. legumes in post-fire regeneration, or by the availability of decomposing litter as an energy source for both aerobic and anaerobic nitrogen fixers.

Since the components of a community cannot grow without amino acids and the nitrogen of the pool depends on fixation, on the average at least replacing that lost from the system by decomposition, then the certainty that some nitrogen fixation will occur will be related to the array of modes in the pathways of nitrogen fixation.

The probability of persistence of the community approaches 1 when the route or pathway diversity is such that there will always be one mode operating under all experienced variations of the environment. Such a condition of diversity would define stability with respect to the nitrogen needs of the ecosystem, i.e. leaks from the system could be replaced by addition to the pool by fixation under all perturbing conditions.

Mineral nutrients are also essential and often limited in supply. Recycling of these nutrients increases their retention time in the system. The pool is replaced by release of pollen, flowering, fruit and seed of deep-rooted plants which gather nutrients from deep weathering profiles or from accumulations of resulting downward leaching of soil solutes. Usually there is more than one route for replenishment of the mineral nutrient pool. In a post-fire situation the loss of mineral nutrients from the system by run-off and rainfall is minimised by the harvest by the root system of freshly grown underground bulbs and tubers and rhizomes or by shrubs with lignotubers or by mycorrhizal fungi. Again there are a number of ways for blocking leaks from the system. Leakage will be least when the diversity of ways of gathering the nutrients released in the post-fire situation is such that at least one route will operate under any conceivable post-fire situation.

In addition to the pathways of fixation there is a tendency for nutrients to accumulate at their place of origin or to fall into sinks, e.g. bogs, lakes, the water table, or even in long-lived vegetation and deep-rooted plants. Herbivores and predators can be looked upon as devices for redistributing these nutrients.

In the sense used here, complexity has to do with variety of modes in the pathways by which biologically important materials are introduced into the system, the different modes of retention and storage, and the ways in which they are redistributed.

Stability

In the foregoing examples diversity and complexity have related to (i) maximising the retention time of expensive biological molecules within a system, and (ii) diversifying the number of modes in routes by which the pool of biologically useful nutrients is introduced into, retained, and redistributed within the system so that a supply and retention is ensured under all possible or conceivable circumstances.

In this sense the community that persists through perturbations or disturbances is successful at achieving diversity in supply and retention and has thereby achieved stability.

At any one instant of time one mode in a route may be more important or efficient than another. At such a juncture the inefficient routes are redundant but stability on a long-term basis may in fact be dependent on the retention of the redundancies. They are in effect insurance policies. Efficiency of use of a resource enhances the retention time by minimising loss through the production of biologically useless degradation products. However, as mentioned earlier, over a long period of time "sinks" will appear within a system and nutrients will accumulate there. Ultimately there will be areas rich in nutrients and others poor in nutrients. In the sense of preserving a community it is advantageous to delay this end, and we can consider mobile animals as devices which delay this end state. Animals such as chironomids or frogs emerging from ponds or moth or other insect larvae from trees or bees distributing pollen or mating flights of ants or termites, or herbivores or predators generally, are to be viewed as devices for delaying the accumulation or redistributing important biological substances.

Management

The problems of management range from the problems associated with natural communities which are being distributed by being isolated as small reserves or invaded by pathogen (*Phytophthora*) to the situations which are physically disturbed such as road verges, or pits left by gravel extraction or bauxite mining. In such disturbed places, a new community may establish but it would take a long time. Nutrients could be added and so hasten the establishment of vegetation—but there is no feed-back if nutrient supply is unbalanced. Moreover, from the theoretical framework developed, the nutrients may have to be replenished repeatedly if the community diversity and complexity necessary for their retention is not present, and replenishment is likely to be a costly and continuing process unless the natural input to the nutrient pool can be balanced with the losses from the pool by means of a suitably diverse and complex community. Finally, stability will only be achieved when supplying pathways are assured under all natural perturbations.

Discussion

In the foregoing I have emphasised that diversity of roles is essential so that retention times of nutrients or replenishment of nutrient pools is maximised under all possible circumstances. Establishment of roles is hard work requiring a great deal of biological insight. However, in addition to the well-known ability of symbionts associated with legumes to fix nitrogen, there is now an extensive and growing literature on nitrogen fixation by plant associations other than with legumes (Silvester 1977) as well as by free-living microbes (Postgate 1971). Of particular interest is the ability of actinomycete symbionts associated with *Casuarina* to fix nitrogen. Actinomycetes appear to be capable of establishing symbiotic relationships with a number of woody shrubs (Silvester 1977) and there may be as yet unrecorded symbioses among the endemic woody shrubs. Shea and Kitt (1976) have indicated the levels of nitrogen fixation by native legumes, while Halliday and Pate (1976) have shown that blue-green algae associated with *Macrozamia* are capable of contributing nitrogen to their host.

Peculiarities of the root systems of Australian Proteacea have been studied for some time (Specht and Rayson 1957, Purnell 1960). Lamont (1972a, b, 1973) has made a detailed study of the proteoid roots of some *Hakea* species, while Lamont and McComb (1974) have studied the role of microorganisms in the formation of proteoid roots and Jeffrey (1967, 1968) has implicated the importance of proteoid roots in phosphorus nutrition.

Additionally fungi are being more and more implicated as important components of ecosystems, both as decomposers and in mycorrhizal associations (Hartley 1959, 1971). Moreover, mycorrhizas are associated with eucalypts (Chilvers and Pryor 1965) and may well be more widespread. Malajczuk *et al.* (1977) have experimentally demonstrated the importance of mycorrhizal infection. Mycorrhizas appear to be important in increasing the area through which solutes can be absorbed. They thus could have an important role in retaining mineral nutrients within the ecosystem, especially where soils are sandy and lack clays on which nutrients might be absorbed and thus physically retained.

The foregoing suggests that natural history observations such as the invasion of gravel pits by *Dryandra* rather than legumes or the invasion of disturbed sandy areas or sand pits on the Swan coastal plain by *Adenanthos* are in some way related to the role of proteoid roots in nutrition. Likewise the ubiquity of *Casuarina* species among the vegetation associations growing on poor sandy soils could indicate the common mode of nitrogen fixation in the system.

Taken together the above suggest that in addition to establishing the roles played by plant species we need also to pay much more attention to the microorganisms of the soil, i.e. the rhizosphere, as well as those that are symbionts on woody plants.

The identification of multiple modes in pathways by which biologically useful materials are introduced into a system, and an assessment of the conditions under which each is optimised, have not been attempted. Nevertheless if segments of the system can be isolated, it is possible in theory to establish measures of species diversity for the different pathways, and ideally measure the contribution of each of these to the circulating pool of biologically important substances. Moreover, it may be possible to establish the robustness of components of these pathways under perturbation. For example, when perturbations occur, there are a number of characteristic sequences for regeneration, as already mentioned: Proteacea *(Dryandra)* but generally not legumes in gravel pits where soil and accumulated nutrients are in poor supply, or legumes in burnt areas where, depending on the intensity of the fire, nitrogen but not minerals will be depleted. Perhaps these characteristics in successional sequences are a manifestation of dominant pathways by which limiting nutrients are being restored to the system.

Thus whilst diversity contributes to the retention time of biologically expensive nutrients in an ecosystem, it is likely that it is the multiplicity of modes in pathways (duplications or redundancies) by which biologically useful molecules are introduced into (blue-green algae, lichens, free-living aerobic and anaerobic microbes, symbiotic actinomycetes and symbiont rhizobia) or retained within (fungi, mycorrhiza, proteoid and other root systems, geophytes and lignotubers which can rapidly produce an extensive root system to scavenge and retain nutrients) the ecosystem which is important for stability of the system. The suggestion is that these redundancies are such that in a stable system at least one mode in each pathway will operate under the conditions of perturbation natural to the system, and natural history observations may give a first clue to the robustness of each mode.

The generalisation for the above example is that under perturbations induced by gravel extraction where depletion of soluble phosphorus is presumed, the phosphorus replenishment mode by way of proteaceous plants is robust, while the nitrogen mode by way of leguminous plants is not. On the other hand, following burning, when the phosphorus pool is intact and the nitrogen pool depleted, the mode of nitrogen fixation by way of symbionts in legumes is robust.

In a community disturbed by the invasion of *Phytophthora*, or where any other cause of catastrophic destruction of vegetation occurs, diversity and complexity are destroyed and no mode in any pathway persists, hence stability is lost.

Management should take into account these functional roles of diversity and complexity, but it is not likely to be easy to develop a complete data base since so much of importance takes place in the rhizosphere.

In summary, the theory developed is based on functional integrity of the ecosystem rather than specific components at any time. It has been assumed that a system cannot sustain itself unless nitrogen is fixed and minerals introduced into the system in quantities which equal losses from the system. Should these biologically important substances be in excess of what the system can use they will be lost, i.e. the system will leak. The presence of a substantial leak suggests that there is an unexploited resource which could be exploited by an organism new to the system. Should this happen, the leak will be stopped and the diversity of the system increased. The assumption is that diversity increases until all serious leaks are stopped.

In addition, the theory suggests that because environments fluctuate seasonally, and suffer other types of perturbation and disturbance, only those persist which contain a variety of modes in the pathways by which biologically important substances are introduced and retained within the system. The variety of modes reflects the complexity of the system. Frequently there are redundancies in modes but functionally the system retains its integrity and tends to return to its former state after perturbations or disturbances. It is the robustness of pathways which endows the ecosystem with stability.

In terms of management of the ecosystem, the compartments that appear to be important are those devoted to the accession of nutrients; the synthesisers (fixation of nitrogen, extraction of mineral nutrients from deep profiles and photosynthesis); the redistribution of nutrients (the animal component of the ecosystem); and the organisms which maximise retention of nutrients within the system (fungi, mycorrhizas and plant root systems generally).

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Peripheral vegetation of Peel Inlet and Harvey Estuary, Western Australia

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Abstract

Fifteen vegetation units, distinguished by differences in the floristic composition of vascular plant species, have been recognised from the Peel Inlet-Harvey Estuary system, Western Australia. Analysis of the epontic diatom flora within units confirms their integrity. The spatial distribution of these vascular-plant communities around the estuarine system appears to be controlled by the substrate summer salinity values, together with the vertical distance from the high water mark. Evidence from aerial photographs extending back 23 years suggests that dynamic processes are less important than these spatial controls in determining community distribution. Exceptions to this occur only when sudden major geomorphic changes force concomitant vegetation changes.

Introduction

During 1977-78 an investigation was undertaken of the peripheral vegetation and associated diatom flora of the Peel Inlet-Harvey Estuary System, Western Australia. This estuarine system comprises two large shallow basins of 65 km^2 (Peel Inlet) and 50 km^2 (Harvey Estuary), joined to the sea by a 5 km inlet channel. The basins are connected to each other by a narrow channel, which cut through a broad, barely submerged marginal shelf. The sedimentology of the area has been described by Logan and Brown (1975). This survey was confined to the tidal marsh environment of both Peel Inlet and Harvey Estuary.

Ecological studies of Western Australian vegetation have shown considerable methodological variation, from empirical analysis of transects (e.g. Sauer 1964), classifications based on dominant strata using a range of criteria (Gardner 1942, Speck 1952, Beard and Webb 1974) to recent implementation of numerical methods utilising floristic information (Havel 1975). This paper outlines the application of the Zurich-Montpellier (Z-M) method as a practical technique utilising floristic attributes. Additionally, the paper evaluates the results from this technique with independently gathered environmental data and data obtained from diatom sampling.

Theoretical implications of Z-M phytosociology have been discussed by Bridgewater (1971), Westoff and van der Maarel (1973) and Muller-Dombois and Ellenberg (1974). These references contain the most detailed accounts of the techniques available in the English language, and it is not proposed to discuss them further in this paper.

Methods

At each of eighteen sites (Fig. 1) two or three transects were laid from the high water mark to the edge of the sandy beach ridge. These sites were considered to represent the least disturbed examples of a variety of soil and vegetational types. Soils of the estuary fringe are referrable to three soil systems—Bassendean and Spearwood Dune systems and Pinjarra Plain soil system (McArthur and Bettenay 1960). Site selection was made by field reconnaissance, coupled with use of colour aerial photography taken in 1976 by the Western Australian Lands Department. The transects comprised regularly spaced relevés (samples) one metre square and spaced 5 or 10 m apart, depending on the abruptness of vegetation change. A total of 747 relevés were collected from the estuaries. Species cover-abundance were recorded for each relevé using the Braun-Blanquet scale (Bridgewater 1971). A set of computer programs was used to print tables of species and relevés for each transect. These tables were then examined, and 'potential differential species' (PDS) noted. The initial choice of PDS is made from species having an apparently clumped distribution, with usually $< 60\%$ presence in the group of relevés forming the transect. Selection of PDS was facilitated using a computer program, which incorporates numerical methods as outlined by Ceska and Roemer (1971). Groups of relevés with similar PDS were then extracted from the transect raw tables and entered into a presence table (Table 1).

Each column in Table 1 represents thus the sum of a number of relevés from the estuary, with the frequency of species presence in these relevés recorded as a percentage class (I-V). Table 1 allows the structuring of a classification for the tidal marsh vegetation (Table 2). As only one locality was surveyed, it is inappropriate to utilise the standard Z-M system of nomenclature. Accordingly, the system of naming the vegetation units follows that of Bridgewater (1974). For ease of reference all specific names are derived from Blackall and Grieve (1974) and Grieve & Blackall (1975).

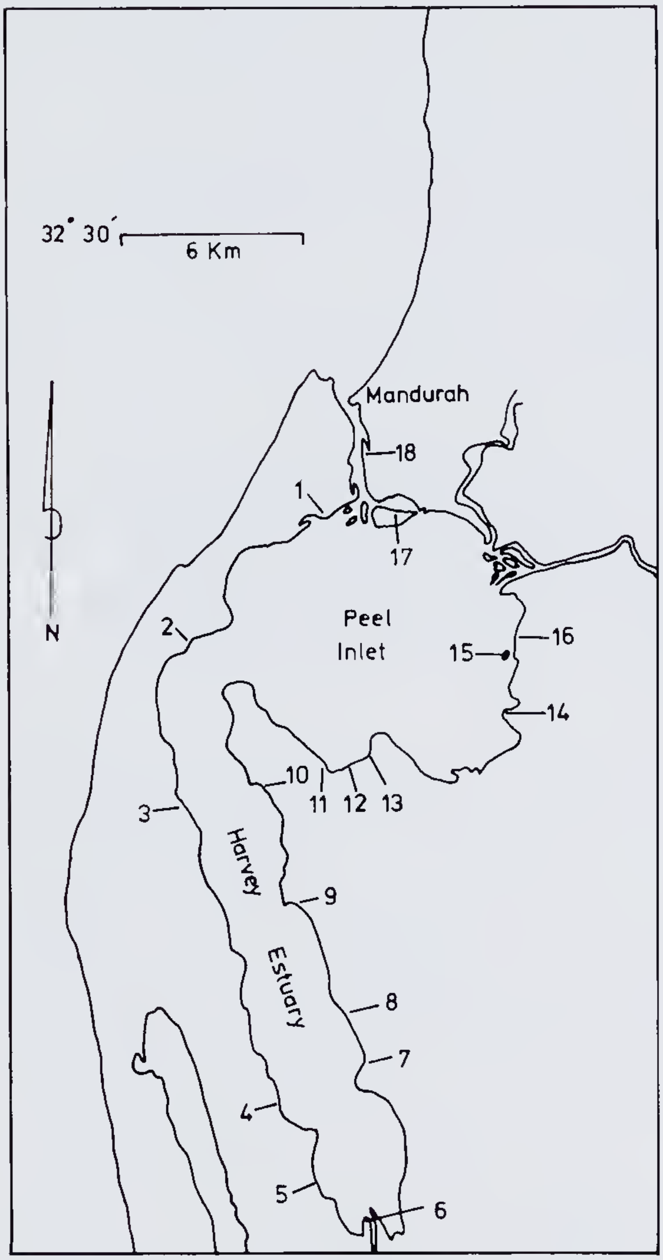

Figure 1.—Location map of Peel Inlet—Harvey Estuary showing sites of transect analysis.

Vegetation ecology

The fifteen vegetation units derived from the classification (Table 2), augmented by all diatom species (Table 3), were subjected to Principal Axes Ordination (van der Maarel 1969). This technique allows a choice of reference stands which will establish the extremes of a gradient instead of emphasizing differences within the groups.

The ordination (Fig. 2) is accompanied by selected substrate information. Summer salinity values were derived from soil samples obtained from the top 10 cm of the soil profile. These were collected during March from all transects, and analysed as a 1:5 soil water extract using a P66 digital chlorodometer. Total ions were measured as a 1:5 soil water extract using a Sproule electronic conductivity meter. This analysis was performed in August. Data were obtained from four replicate sites for each vegetation group.

The Y axis of the ordination appears to relate strongly to salinity, with hypersaline relevés at the positive end and slightly brackish relevés at the negative. The relationship of relevés along the X axis is less easily discernable, but approximates to a littoral—beach ridge sequence.

Vegetation distribution and dynamics

Peripheral vegetation of an estuary is influenced by marked variations in substrate conditions in both space and time. Horizontal distance from the littoral zone and vertical distance from a fluctuating water table are two important factors superimposed on other influences. Environmental factors may occur either as a mosaic, or as an attenuating gradient, depending upon local conditions. An understanding of the spatial relationships of vegetation with these environmental factors may help in elucidating temporal processes operating within estuarine vegetation. Figure 3 shows the distribution of physical features, vegetation units and salinity regimes along a hypothetical transect from water edge to established dunes.

Distribution of the *Arthrocnemum* complex component communities reflect both spatial and temporal sequences which are readily observed in numerous salt marshes of the area. The *Arthrocnemum bidens* community develops on the less saline rims of salt marsh concavities, but progrades into the *Triglochin mucronata* community at lower levels. In the more saline centres of the concavities, *A. halocnemoides* occurs as a single species, or in extreme environments, a bare pan develops. Where the concavities are less saline, perhaps as a result of more effective ground water or tidal flushing the *Salicornia quinqueflora* community occurs. Sedimentation of the concavity and subsequent reduction of flushing implies a maturation of the system through time. Where the concavity is linked to the estuary, the *Arthrocnemum* complex merges with the *Salicornia* complex.

Beeftink (1962) found the salinity units of the Venice system useful in environmentally classifying saltmarsh communities. This system provides a classification of saline waters into three broad categories—euhaline, with a range of 1.65-2.2% chlorinity, polyhaline, with a range of 1.0-1.65% chlorinity, and mesohaline, with a range of 0.3-1.0% chlorinity. Vegetation units 1-3 (*Arthrocnemum* complex) are euhaline, using this terminology, while the *Triglochin mucronata* and *Salicornia quinqueflora* communities (units 4 and 5) are polyhaline, with all other communities being mesohaline.

Many communities clearly respond to spatial features, such as the salinity changes described above, rather than temporal factors. Nevertheless, due to the dynamic nature of shorelines in this region, it is possible to infer some successional relationships between communities. Inference may be given a factual basis by comparison of old aerial photographs with recent runs. In this study aerial photographs from 1957 allowed a time scale to be placed on some successional processes.

Initial development of tidal marshes can be linked to emergence of spits or sandbars. Sedimentation often continues until the bar is joined to the shore by one extremity (Chapman 1938). Once sufficient

Table 1.

Presence table for important species in the 15 vegetation units

Vegetation units (see Table 2)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Arthrocnemum halocnemoides	V	V	V	V	I	+	....	....	....	....	II	II	....	....	....
Salicornia quinqueflora	....	I	V	II	V	V	V	IV	V	....	III	....	....	....	....
Suaeda australis	....	....	....	....	I	V	I	+	III	+	III	....	II	....	....
Juncus maritimus	....	....	....	....	....	III	IV	V	....	III	I	....	V	....	....
Machaerina juncea	....	....	....	....	....	....	I	+	V	III	....	....	....	....	....
Melaleuca raphiophylla	....	....	....	....	I	II	....	....	IV	III	....	....	....	....	....
Schoenus fasicularis	....	....	....	....	....	....	....	....	I	IV	....	....	....	....	....
Apium prostratum	....	....	....	....	....	....	....	....	....	IV	....	....	....	....	....
Sporobolus virginicus	....	+	....	....	III	I	I	+	....	IV	IV	....	I	....	V
Atriplex paludosa	....	....	....	....	....	I	....	....	I	....	V	V	....	....	....
Parapholis incurva	II	....	....	....	+	....	....	....	....	....	II	....	....	V	V
Cotula coronopifolia	....	....	....	....	....	....	....	....	....	....	....	....	....	V	IV
Arthrocnemum bidens	V	+	....	....	....	I	....	....	....	....	....	....	....	III	III
Triglochin mucronata	....	+	+	V	....	....	....	....	....	....	....	....	....	....	....
Gahnia trifida	....	....	....	....	....	+	V	+	II	+	....	....	....	....	....
Frankenia pauciflora	I	I	I	II	+	....	....	....	....	....	IV	....	....	I	....
Atriplex hastata	....	....	....	....	+	I	....	....	....	+	+	V	II	II	....
Polypogon monspeliensis	....	+	....	....	+	I	....	....	III	II	....	V	....	V	....
Angianthus preissianus	I	I	....	III	+	....	....	....	....	....	....	....	....	....	IV
Casuarina obesa	I	....	....	III	II	....	I	I	....	....	....	....	....	I	I
Hordeum hystrix	....	+	....	III	....	....	....	....	....	+	....	....	....	II	....
Melaleuca cuticularis	....	....	+	....	+	I	II	III	III	....	II	....	I	....	....
Samolus juncea	....	....	+	III	....	+	....	III	II	II	....	....	....	....	....

Note: I = species occurred between 0-19% of relevés taken.
II = species occurred between 20-39% of relevés taken.
III = species occurred between 40-59% of relevés taken.
IV = species occurred between 60-79% of relevés taken.
V = species occurred between 80-100% of relevés taken.
\+ = species occurred in only one relevé taken.

N.B. Species which occurred in less than 5 of the total relevés are not included in this table.

protection is afforded, the pioneer community appears to be the *Salicornia quinqueflora* community, often with *S. quinqueflora* as the only species represented. As the surface is stabilised, and raised a little by silt accumulation, the *Salicornia* community is replaced by the *Salicornia-Suaeda australis* community. A tidal marsh of these two communities now exists north of Heron Point, Harvey Estuary. That this marsh has developed within 20 years is established by comparison of aerial photographs for 1957 and 1976.

Marshes colonised by *Arthrocnemum* species are more saline, tend to be completely summer dry and certainly have a better developed soil profile than the early colonising spits and sandbars. It seems likely that the *Arthrocnemum* community represents a stable environment, which could be regarded as climax vegetation. Most of the communities identified appear more correlated with estuarine and fluvial processes, rather than the base soil system. Exceptions to this appear to be the *Salicornia-Machaerina* and *Schoenus-Sporobolus* communities which are apparently confined to shores of the Spearwood Dune system.

Diatom communities

Little work has been done in Australia on the diatom flora of estuaries and salt marshes, with Wood (1964) being the most significant contribution. Diatoms form an important part of the food chain in estuaries, with some species also useful as environmental indicators. Associations of distinct diatom communities with terrestrial and macro-algal communities in salt marshes and estuaries have been noted by Carter (1948), Round (1960) and Chapman (1962).

Table 2.

Classification of vegetation units

I. *Arthrocnemum halocnemoides* complex
   1. *Arthrocnemum bidens* community
   2. *A. halocnemoides* community
   3. *Salicornia quinqueflora* community
   4. *Triglochin mucronata* community

II. *Salicornia quinqueflora* complex
   5. *S. quinqueflora* community

III. *Salicornia quinqueflora—Suaeda australis* complex
   6. *Suaeda australis* community

IV. *Juncus maritimus—Salicornia quinqueflora* complex
   7. *Gahnia trifida* community
   8. *Juncus maritimus—Salicornia quinqueflora* community

V. *Salicornia quinqueflora—Machaerina juncea* complex
   9. *Salicornia quinqueflora—Machaerina juncea* community

VI. *Schoenus fasicularis—Sporobolus virginicus* complex
   10. *Schoenus fasicularis—Sporobolus virginicus* community

VII. *Atriplex paludosa* complex
   11. *Frankenia pauciflora* community
   12. *Atriplex hastata* community

VIII. *Juncus maritimus* complex
   13. *Juncus maritimus* community

IX. *Cotula coronopifolia—Parapholis incurva* complex
   14. *Polypogon monspeliensis* community
   15. *Sporobolus virginicus—Angianthus preissianus* community

Vegetation units denoted by arabic numerals refer to the numbered columns in Table 1.

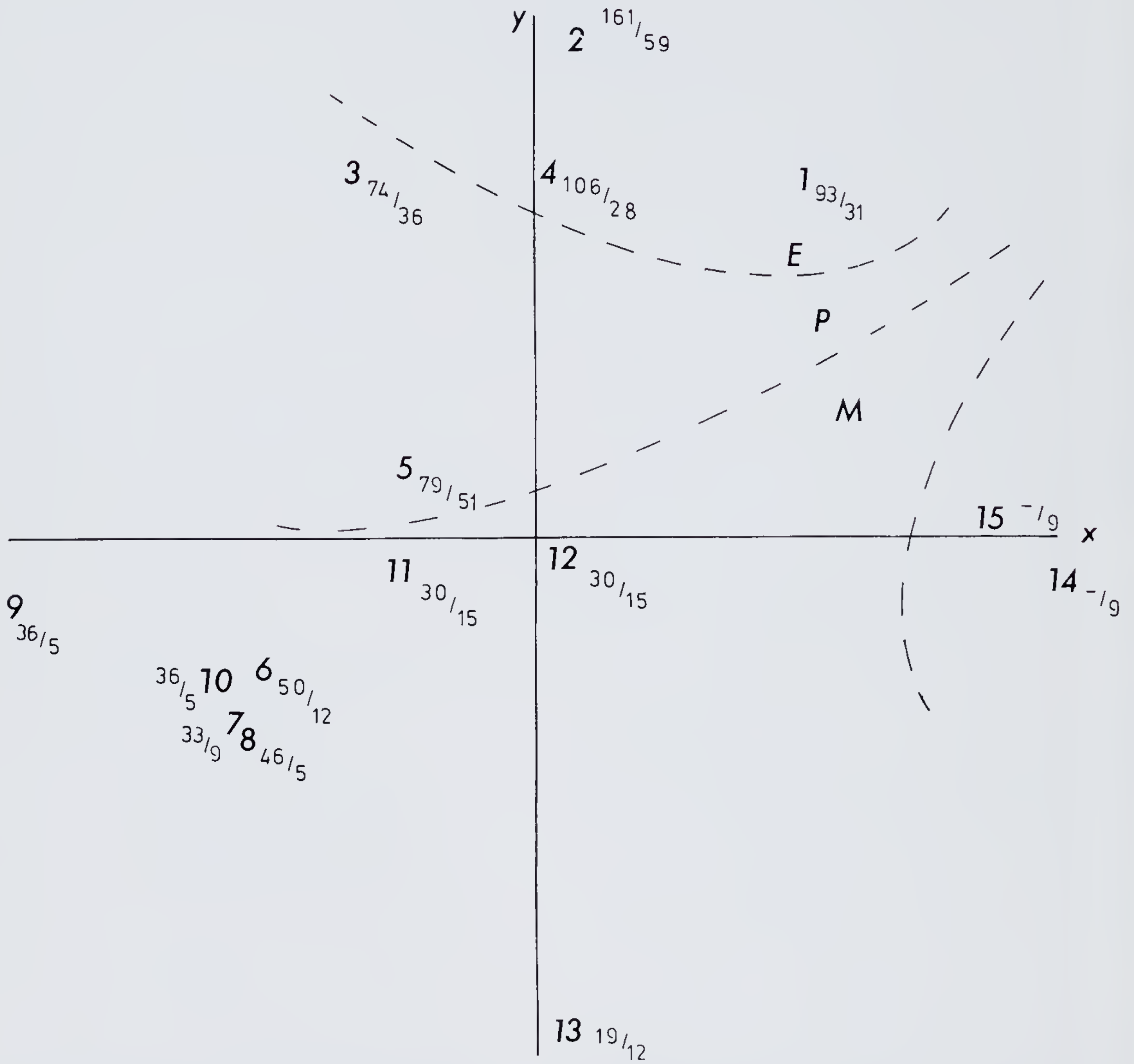

Figure 2.—Principal Axes Ordination of the 15 vegetation units. Figures in bold type represent vegetation units. (see Table 2). Figures in lighter type represent values for chlorinity and total ions (Meq. L^{-1}/μMhos x 10^{-2}). Dashed lines define salinity, where E equals euhaline, P equals polyhaline and M equals mesohaline.

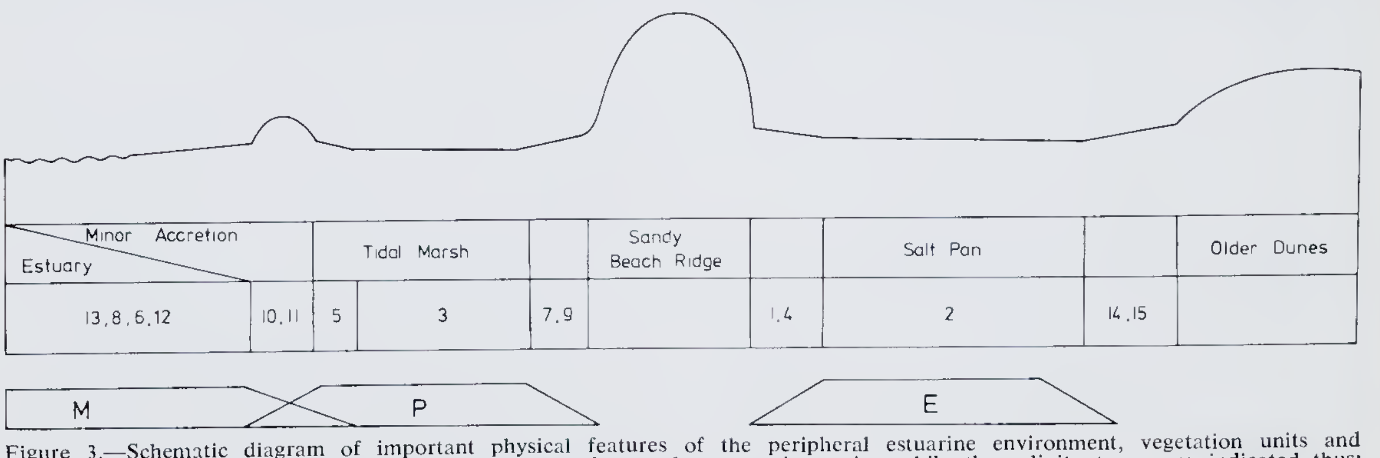

Figure 3.—Schematic diagram of important physical features of the peripheral estuarine environment, vegetation units and salinity types along a hypothetical transect. Figures denote the vegetation units, while the salinity types are indicated thus: M equals mesohaline, P equals polyhaline, E equals euhaline.

Diatom communities and floristically defined vascular plant communities may well be affected by different environmental conditions. Aleem (1950), however, showed that benthic diatoms seldom penetrate deeper than 2 mm into the marsh surface. Diatoms form a micro-habitat of mucilage on the surface of salt marshes in the Peel-Harvey system, so they could be buffered to some extent from the high salinity levels in the soils of the mature marshes. Planktonic forms may also be temporarily deposited in benthic conditions, and, if sampled, could conceivably affect the results obtained. With these caveats in mind, an analysis of diatoms found in each of the 15 vegetation units was attempted.

Four widely distributed replicate sites were chosen for each of the vegetation units noted in Table 2. Soil surface scrapings from each site were cultured in petri dishes in the laboratory. A sterilised solution of sugar and yeast extract was applied as required, to keep the scrapings moist for a period of three weeks before being examined. In this way, species dormant in the soil were encouraged to become active and more readily observed.

Table 3.

Diatom species located in vegetation units

	Vegetation units (see Table 2)														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Achnanthes longipes Agardh	+	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Mastoglia ignorata Hust.	+	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Amphora javanica A.S.	+	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Navicula marina Ralfs in Pritchard	+	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Cocconeis speciosa Gregory	+	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Nitzchia sp. 6	....	+	....	....	....	....	....	....	....	....	....	....	....	....	....
N. longissima (de Brebisson ex Kutz) Ralfs in Pritchard	....	+	....	....	....	....	....	....	....	....	....	....	....	....	....
Diploneis crabro Ehr.	....	+	....	....	....	....	....	....	....	....	....	....	....	....	....
Nitzchia subvitrea Hust.	....	....	....	+	....	....	....	....	....	....	....	....	....	....	....
Diploneis sp. 1	....	....	....	+	....	....	....	....	....	....	....	....	....	....	....
Nitzchia vitrea Norm.	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Cymbella subturgida Hust.	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Navicula sp. 1	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Cocconeis distans A.S.	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Nitzchia sigma var. *rigida* Grun. ex Van Heurck	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Achnanthes sp. 2	....	....	....	....	+	....	....	....	....	....	....	....	....	....	....
Amphiprora angustata Hendey	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Achnanthes sp. 3	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Opephora sp. 1	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Synedra sp. 1	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Anomoenis sp. 1	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Genus A	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Plagiogramma sp. 1	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Nitzchia closterium (Ehr.) Wm. Smith	....	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Amphora gigantea Grun. in A.S.	....	....	....	....	....	....	....	....	+	+	....	....	....	....	....
Genus B	....	....	....	....	....	....	....	....	....	....	+	+	....	....	....
Mastoglia sp. 2	....	....	....	....	....	....	....	....	....	....	+	+	....	....	....
M. pseudoparadoxia Hust.	....	....	....	....	....	....	....	....	....	....	+	+	....	....	....
Navicula sp. 2	....	....	....	....	....	....	....	....	....	....	+	+	....	....	....
N. vulpina Kutz.	....	....	....	....	....	....	....	....	....	....	....	....	+	....	....
Fragillaria sp. 1	....	....	....	....	....	....	....	....	....	....	....	....	+	....	....
Nitzchia gracilis Hantz.	....	....	....	....	....	....	....	....	....	....	....	....	+	....	....
N. sp. 4	....	....	....	....	....	....	....	....	....	....	....	....	+	....	....
Diploneis smithii (de Brebisson) Cleve	....	....	+	+	....	....	....	....	....	....	....	....	....	....	....
Nitzchia sp. 1	....	....	+	+	....	....	....	....	....	....	....	....	....	....	....
Navicula elegans Wm. Smith	....	....	+	+	....	+	....	+	....	....	....	....	....	....	....
Nitzchia brebissonii Wm. Smith	+	....	....	....	+	....	....	....	....	....	....	....	....	....	....
N. sp. 5	+	....	....	....	+	+	....	....	....	....	....	....	....	....	....
Amphora proteus Gregory	+	....	....	....	+	+	....	....	....	....	....	....	....	....	....
Achnanthes brevipes Agardh	....	....	....	....	+	+	....	....	....	....	....	....	....	....	....
Amphora macilenta Gregory	....	....	....	....	+	+	....	....	....	....	....	....	....	....	....
Cocconeis scutellum Ehr.	....	....	....	....	+	+	....	....	....	....	+	+	....	....	....
Thalassothrix sp. 1	....	....	....	....	+	+	....	....	....	....	+	+	....	....	....
Cocconeis debesi Hust.	....	....	....	....	....	+	....	....	....	....	+	+	....	....	....
Epithemia sp. 1	....	....	....	....	....	+	....	....	....	....	+	+	....	....	....
Cocconeis apiculata A.S.	....	....	....	....	....	+	....	....	....	....	+	+	....	....	....
Navicula sp. 3	....	....	....	+	+	....	....	....	....	....	+	+	....	....	....
Nitzchia compressa (Bail.) Boyer	+	....	....	+	....	+	....	....	....	+	+	+	....	....	....
Pleurosigma strigosum Wm. Smith	....	+	....	+	+	....	....	....	....	....	+	+	....	....	....
Epithemica sp. 2	....	....	....	....	....	+	....	....	....	....	+	+	+	+	+
Achnanthes sp. 1	....	....	....	....	....	....	....	....	....	....	....	....	+	+	+
Grammatophora macilenta Wm. Smith	+	....	....	+	+	....	....	....	....	....	....	....	....	+	+
Pinnularia legumen Ehr.	+	....	....	....	+	+	....	....	....	....	....	....	....	....	....
P. splendida Hust.	+	....	....	....	....	+	+	....	....	....	....	....	....	....	....
Cocconeis placentula Ehr.	+	....	....	....	....	+	....	....	....	....	....	....	....	....	....
Navicula lyra var. *elliptica* A.S.	+	....	+	+	+	+	+	....	....	....	+	+	....	....	....
Pinnularia ambigua Cleve	+	....	+	+	....	....	+	+	....	....	+	+	....	....	....
Amphora graeffii (Grun.) Cl.	+	+	....	+	....	+	....	+	....	....	....	....	....	....	....
A. sp. 2	....	+	+	....	....	+	+	+	....	....	....	....	....	....	....
Nitzchia sp. 2	....	+	+	....	....	....	+	....	....	....	....	....	....	....	....
N. sp. 3	....	....	....	+	+	....	....	+	....	....	....	....	....	....	....
Melosira sp. 1	....	....	....	....	....	+	....	+	....	....	....	....	....	....	....
Cymbella yarransis A.S.Cl.	+	....	....	+	....	....	....	....	....	....	....	....	....	....	....
Genus C	+	....	....	....	....	....	....	+	....	....	....	....	....	....	....
Cocconeis sp. 1	....	....	+	....	....	+	....	....	....	....	....	....	....	....	....
Grammatophora marina (Lyngb.) Kutz	....	....	....	+	....	+	....	....	....	....	....	....	....	....	....

Where species identification was not possible a code name was used. Descriptions and drawings of unidentified diatoms may be found in Backshall (1977), or copies may be acquired from the authors. Identification of species was achieved using the following works: Crosby and Wood (1959), Wood *et al.* (1959), Wood (1961a, 1961b, 1963) and Hendey (1964).

The distribution of diatoms (Table 3) shows that more than 50% of the species were unique to individual vegetation units, although approximately half of these were accounted for by groups 1, 5, and 6. Unique species present in groups 2 and 4 add justification for distinguishing these vegetation units. Groups 10, 11, 14, 15 are, however, distinguished only by their paucity of diatom flora. This is probably a reflection of long periods of surface desiccation on these more elevated sites. *Nitzchia compressa, Cocconeis placentula, Pinnularia legumen* and *P. splendida* indicate some affinity between groups 1 and 6. The *Arthrocnemum bidens* community (group 1) is typically found on the emerging fringes of salt marsh concavities, while *Salicornia-Suaeda* community (group 6) occupies a similar zone on the emerging banks of the estuaries. The suggested similarities may be because the communities occupy sites of regular water fluctuation while differences in salinity of these 2 habitats appear to be reflected by differences in the diatom flora of the communities. Similarly, although the *Salicornia-Suaeda* community and the *Salicornia quinqueflora* community may have unique species of diatoms, a clear relationship between them is indicated by the common presence of *Amphora proteus, Nitzchia* sp. 5, *Cocconeis scutellum, Achnanthes brevipes, Amphora macilenta* and *Thalassiothrix* sp. 1. Both vascular-plant communities are found at similar elevations above high water mark, but with different soil salinities.

The overall distribution of diatom species is similar to that reported by Round (1960) with many species exhibiting a strong preference for different habitats, while others demonstrate a wider tolerance. Lack of the common planktonic genera *Rhizosolenia, Chaetocerous* and *Coscinodiscus* would seem to confirm that the species encountered are indicative of surface changes, rather than planktonic drift-ins.

Interaction of peripheral and submerged vegetation

One of the major environmental problems in the Peel-Harvey system is high productivity of the alga *Cladophora*. During winter storms massive amounts of algal material are deposited on shorelines, often with severe results on the *Juncus maritimus* complex. Massive deposition can cause death or debilitation of the *Juncus* and consequent erosion. Colonisation of the large masses of *Cladophora* is often effected by *Atriplex* spp. and *Suaeda australis*. This latter species commonly colonises organic deposits, e.g. *Zostera* deposits at Westernport Bay, Victoria.

At some points on the shores of Peel Inlet *Scirpus maritimus* appears to also colonise areas of light *Cladophora* deposition. There appears to be a competitive interaction between *S. maritimus* and *J. maritimus* on these sites which warrants further investigation. Degradation of the established *Juncus maritimus* community will inevitably result in shoreline regression, and consequent build-up of silt in other sites.

This effect is another problem associated with the occurrence of *Cladophora* mats. Regeneration of the shoreline appears rapid in regions where the *Salicornia quinqueflora—Suaeda australis* community occurs (i.e. in areas where shoreline stabilization is proceeding naturally), but is lacking on the eastern shore of Peel Inlet. The introduction of colonising species (e.g. *Suaeda australis, Atriplex hastata*), into freshly deposited *Cladophora* mats could be a useful management tool in preventing erosion, and aiding rapid assimilation of the *Cladophora*.

Acknowledgements.—Thanks are due to Mr. J. Johns for assistance with diatom taxonomy, and Mr. P. Wilson for discussions on the Chenopodiaceae of the south-west. Dr. R. Fields provided valuable background data for the study area. Special thanks are due to Ms. K. Gom and Ms. J. Jolly for typing and cartographic assistance.

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Obituary

Leslie William Samuel 1908-1980

L. W. (Les) Samuel, former Director of the Western Australian Government Chemical Laboratories, died on 20 July 1980. He was educated at Perth Modern School, the University of Western Australia and the University of London and was one of the many Modern School students of that era to become prominent in the professional life of the State.

After graduating B.Sc, he worked for a short period in the Department of Agriculture under Dr. L. J. H. Teakle on soil surveys, before obtaining a Hackett Studentship in 1933 to do a Ph.D. at the University of London. His supervisor at London University was Sir John Russell, Director of Rothamsted Experimental Station, who wrote to the Chancellor of the University of Western Australia saying "We found Samuel to be a diligent and capable investigator, a good manipulator in the laboratory and a clear thinker in seeking interpretation of his results".

Returning to the Western Australian Department of Agriculture in 1935 he became a cereal chemist and for many years was a judge of bread at the Perth Royal Show. In 1947 he became Deputy Government Agricultural Chemist in the Government Chemical Laboratories and was promoted to Director in 1957, in which position he remained until his retirement in 1973. During his seventeen years as Director he considerably increased the influence of the Laboratories in the community.

He was a man who lived for his work and in all his 40 years in the State Public Service, he took only a months long service leave and very little of his annual leave. His ability as a clear thinker, perceived early by Sir John Russell, remained with him all his life. His scientific approach and integrity, and his ability to be nearly always right won him the respect of those with opposing views, even if many did not appreciate being proved wrong. He was a strong supporter of his profession and joined the Royal Australian Chemical Institute as an Associate in 1930. He was made a Fellow in 1948 and was honoured further by being elected a Fellow of the Royal Institute of Chemistry.

He joined the Royal Society of Western Australia in 1931 and served on the Council from 1957-1969. He was elected an Honorary Life Member in 1977. Although an active worker for the Society on sub-committees and as Hon. Auditor for more than 20 years he declined to take the office of President. Dr Samuel was a Fellow of ANZAAS for many years and was a foundation member of the Australian Institute of Agricultural Science. He worked actively for these organisations, but again declined to hold any executive positions.

Les Samuel will long be respected and remembered by his friends, colleagues and associates, and many scientific organisations will be the poorer without his penetrating comments and constructive criticisms.

R.C.G., C.F.H.J.

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Preliminary observations of behavioural thermoregulation in an elapid snake, the dugite, *Pseudonaja affinis* Gunther

by H. Saint Girons* and S. D. Bradshaw

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Abstract

Biotelemetry was used to study the behavioural thermoregulation of an adult dugite *(Pseudonaja affinis)* which was confined in a large external enclosure. At the start of digestion the dugite regulated its body temperature at 32.9 ± 0.21°C and this fell within a few days to 32.2 ± 0.09°C ($p < 0.01$) which appears to correspond to the range for the preferred body temperature (PBT) for this species. Throughout the period of observation the snake periodically allowed its body temperature to rise above the PBT, when exploring the enclosure or searching for food, and this often exceeded 34°C with 35.4°C being the maximum temperature voluntarily tolerated. As periods of thermoregulation and searching alternated throughout each day, the overall mean body temperature recorded was higher than the PBT and equalled 33.6 ± 0.23°C at the start and 32.4 ± 0.12°C at the end of the period of digestion.

Introduction

Studies of behavioural thermoregulation in reptiles have concentrated almost exclusively until recently on lizards (see Templeton 1970 for a review) but the development of suitable biotelemetric techniques has resulted in an increasing number of studies devoted to snakes (McGinnis and Moore 1969, Osgood 1970, Johnson 1972, Naulleau and Marquès 1973, Bui Ai *et al.* 1975, Saint Girons 1975, 1978, Shine 1976). However, information on the thermal preferences of Australian elapid snakes is extremely meagre and fragmentary (see Heatwole 1976 for a bibliography) and this motivated us to make some preliminary observations on a single large specimen of the dugite *(Pseudonaja affinis)* held in captivity in Perth, Western Australia.

Materials and methods

The observations were carried out on an adult male dugite *(Pseudonaja affinis)* captured on 9 November 1978 at the University of Western Australia's Marsupial Breeding Station at Jandakot. The snake was placed the next day in a large enclosure (3.5 x 2.5m) which had a sand base and was furnished with a variety of stone shelters and two large basins containing water. The enclosure was in the shade of surrounding trees each day between 0800 and 0855 h and from 1430 h onwards. Another smaller dugite and two tiger snakes *(Notechis ater)*, all captured on the same day at Jandakot, were also housed in the same enclosure. On 16 November the large dugite, which had settled down well in the enclosure and was no longer disturbed by the presence of observers, swallowed at 1045 h a dead mouse containing a temperature-sensitive radio transmitter (Model V, Mini-Mitter Co. Inc., Portland, Oregon). The dugite ate a second mouse at 0900 on 17 November and the observations were terminated at 1800 h on 20 November. The dugite was encouraged to regurgitate the transmitter by gentle manipulation and at this stage the second mouse was almost completely digested.

The transmitter was calibrated in water with a Schultheis thermometer, before and following its implantation in the dugite. The pulse rate varied linearly between 0°C and 50°C and the signal was received with a small commercial transistor radio. The number of pulses per 30 seconds were counted, using a stopwatch, and subsequently converted to give the body temperature of the animal. The transmitter used had a useful range of approximately 1m and antennae were placed on the ground inside the enclosure to facilitate reception of the signal when the dugite was moving about. In total, 181 measurements of the body temperature of the snake were recorded, 128 of these on 18 and 19 November when the animal was kept under continuous observation. Mean temperatures were calculated from the values recorded when the enclosure was in full sunlight and the animal was thus provided with a suitable gradient for thermoregulation. Data from periods when the enclosure was in shade are shown in Figure 1, but were excluded when calculating mean body temperatures.

The statistical significance of differences between mean body temperatures was assessed using Student's t-test and a probability of less than 0.05 was taken to indicate significance.

Results

The dugite emerged from its nocturnal shelter as soon as this was touched by the first rays of sunlight in the morning (at approximately 0715 h)

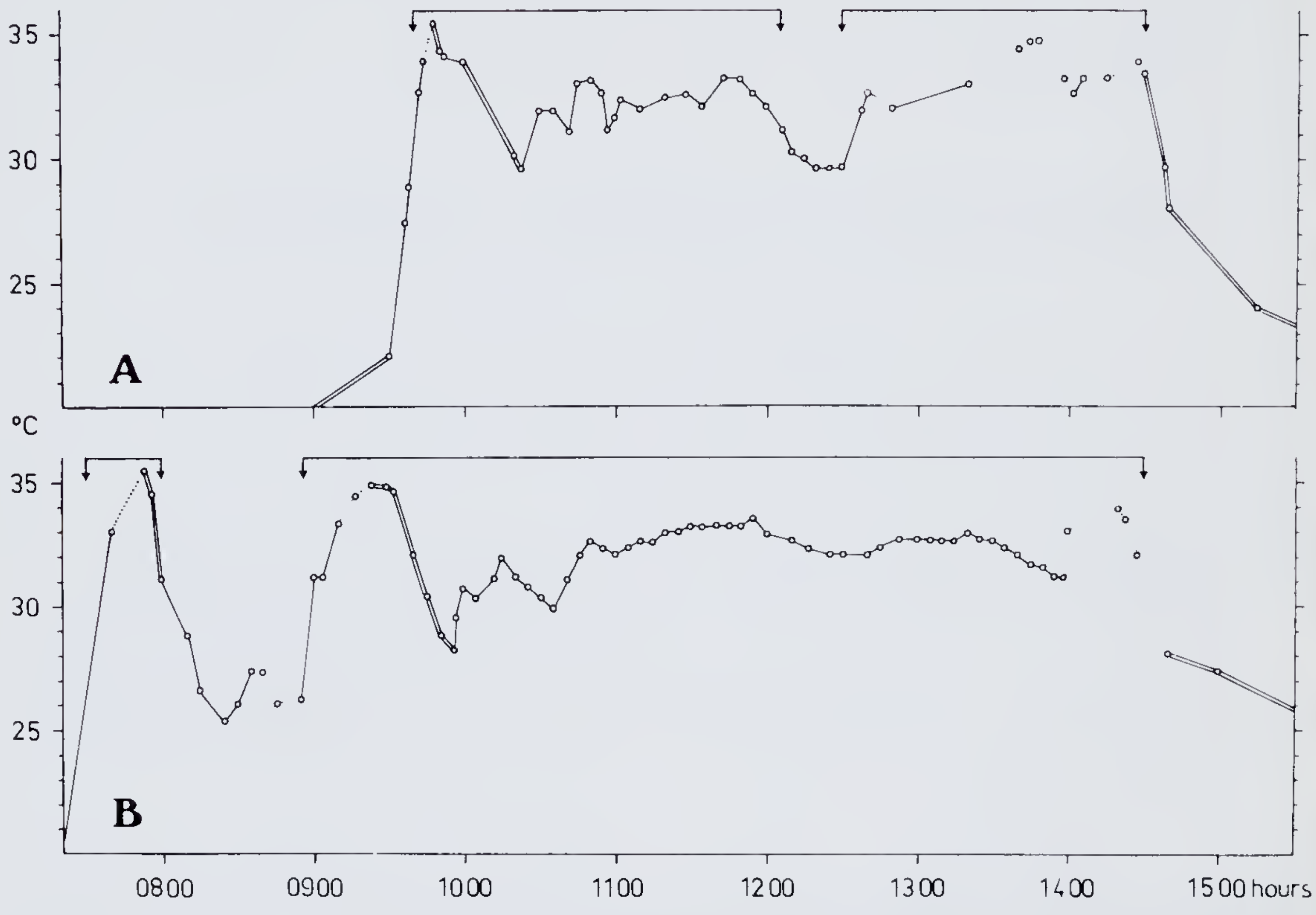

Figure 1.—Body temperature throughout the day of a large male dugite *(Pseudonaja affinis)* confined in an external enclosure on (A) 18 November 1978 and (B) 19 November 1978. The arrows (↓ ↓) indicate the times between which the enclosure was in full sunlight and the animal was thus provided with a large thermal gradient: (====) period when the snake was in its shelter; (———) periods when the snake was engaged uniquely in thermoregulatory behaviour; (.......) periods when the snake actively explored the enclosure in search of food

with a body temperature between 18°C and 22°C, depending upon the day. During most of the time when the sun was shining the animal was engaged in thermoregulatory activity, either resting in the shade or exposing a variable portion of its body to the sun's rays, usually at the entrance to its shelter. Under these conditions the body temperature did not vary by more than 3.6°C, the preferred body temperature (PBT) being 32.9 ± 0.30°C on 17 November, the day after swallowing a mouse, and this fell to 32.2 ± 0.37°C by 20 November by which time the process of digestion was much more advanced, the difference between these two means not being statistically significant (see Table 1). If however one compares the pooled mean for November 16 and November 17 (32.9 ± 0.21°C) with the overall mean for November 18-20 (32.2 ± 0.09°C), then this decline is statistically significant with $p < 0.01$.

Shade from nearby trees fell over the enclosure by 1430 h each day and the snake always returned to its shelter by 1500 h. Subsequently it would emerge infrequently and then only for brief periods in the late afternoon. At different periods of the day, usually between 0730 h and 1000 h and between 1300 h and 1500 h, the dugite would actively explore the enclosure attempting to burrow beneath all the stones and water containers. These activity periods, which were apparently motivated by a search for food, could be set off at any time of the day simply by the odour of a dead mouse and were observed at body temperatures ranging from 26.0°C to 34.9°C. During these periods the snake did not attempt to regulate its body temperature which consequently increased rapidly when the animal was in full sunlight up to a temperature of 35.4°C which corresponded to the maximum voluntarily tolerated. On reaching this temperature the animal would either move into the shade or, more often, return to its shelter whereupon its body temperature would fall rapidly, generally to a level much lower than the PBT, as if to compensate for the period of overheating. Only later would the dugite re-emerge partially and resume its normal thermoregulatory behaviour. Figure 1 gives a number of clear examples of such behaviour.

During nine such exploratory periods observed between 16-19 November, the mean body temperature of the dugite fell four times between 34.5 and 35.0°C and the mean recorded for the other five periods were respectively: 35.2°C, 34.3°C, 33.9°C, 32.1°C and 26.7°C. From these observations it would appear that such exploratory or food-seeking behaviour in the dugite is reasonably temperature-independent between the maximum voluntarily tolerated (35.4°C) and some minimum temperature which is probably

Table 1

Mean body temperatures (°C) and range for the dugite, Pseudonaja affinis, *during periods of exclusive thermoregulation (PBT) and overall, including exploratory and food-seeking, behaviour.*

Date (1978)	Preferred Body Temperature (PBT)	Range	Overall Mean Body Temperature	Range
16 Nov.	32·8 ± 0·15 (5)	32·3–33·2	33·7 ± 0·34 (10)	32·3–35·4
17 Nov.	32·9 ± 0·30 (12)	31·1–34·4	33·5 ± 0·31 (17)	31·1–35·4
18 Nov.	32·4 ± 0·67 (25)	31·1–33·2	32·8 ± 0·19 (40)*	29·6–35·4
19 Nov.	32·1 ± 0·95 (47)	29·6–33·5	32·3 ± 0·18 (64)**	28·0–35·4
20 Nov.	32·2 ± 0·37 (11)	31·5–32·9	32·2 ± 0·37 (11)*	31·5–32·9

Data given as mean ± S.E., number of observations in parentheses. Statistical significance of differences between means are given relative to the mean on the first day (16 November 1978) with * $p < 0·05$ and ** $p < 0·005$.

lower than 26°C. Such activity is limited nevertheless by the rapidity with which the animal attains its maximum temperature voluntarily tolerated during sunny periods of the day and this renders such exploratory activity virtually impossible during the hottest periods of the day, even in spring.

Since the body temperature tended to rise towards the maximum voluntarily tolerated whenever the animal was active and searching, the overall mean of all the body temperatures recorded when it was possible for the dugite to thermoregulate is almost certainly higher than the PBT. This overall mean was 33.6 ± 0.23°C for 16-17 November and 32.4 ± 0.12°C from 18-20 November (see Table 1), the difference between the two means being statistically significant with $p < 0.001$. The average PBT calculated at the beginning of the period of digestion (16-17 November) was 32.9 ±0.21°C and 32.2 ± 0.09°C over the period 18-20 November, when the period of digestion was more advanced, the difference between these two means being statistically significant with $p < 0.005$.

Discussion

In their now classic study of the behavioural thermoregulation of desert reptiles, Cowles and Bogert (1944) recognised a "basking range" and a "normal activity range" falling between the minimum and maximum temperatures voluntarily tolerated. Within the normal activity range they identified a "preferred" body temperature (PBT) for each species, which they also called the optimum or "eccritic" body temperature, corresponding to the mean of the body temperatures recorded when the animal is provided with a sufficiently extensive temperature gradient. Subsequently, many workers (e.g. Brattstrom 1965) have tended to confuse this PBT with the average body temperature of animals captured randomly throughout the day in the field, and taken usually with little regard for the specific behaviour of the animal at the time. Heath (1964) and Licht *et al.* (1966) where amongst the first to point out that such average body temperatures are misleading, comprising as they do, measurements from animals involved in a variety of activities, including basking when the body temperature has not yet attained the PBT. In many cases, although the animals may be active, the prevailing conditions may also be such that it is impossible for them to attain their PBT and Licht *et al.* (1966) and Bradshaw and Main (1968) noted a number of discrepancies between such field body temperatures and the temperature chosen by the same animals in a photothermal gradient in the laboratory. The problems associated with the measurement of the PBT are now better appreciated and have been recently discussed in the literature (see Saint Girons 1975, Heatwole 1976, Werner and Whitaker 1978).

In the case of *Pseudonaja affinis,* it is clear that so long as the snake is provided with a sufficiently broad thermal gradient it will maintain its body temperature within relatively narrow limits and the PBT of the animal studied varied little over a period of five days, being approximately 33°C at the beginning of digestion and 32°C at the end. The minimum temperature voluntarily tolerated is almost certainly lower than the lowest temperature recorded during the study (18°C) and the normal activity range for the dugite would appear to be between 26°C and 35.4°C, the latter representing the highest temperature voluntarily tolerated by this individual. Obviously the study of further individuals will modify this range somewhat but the above are probably reasonable estimates of these parameters for this species. The temperature range is very close to that of *Coluber flagellum (Masticophis flagellum),* a diurnal Colubridae living in comparable semi-arid regions of the Mediterranean, for which Cowles and Bogert (1944) found a normal activity range from 27 to 35°C, a PBT of 33°C and a maximum temperature voluntarily tolerated of 37°C. Other specific comparisons are difficult to make, because of the variety of techniques employed by various workers and the frequent confusion between the PBT and the average field temperature of active animals, but it would appear that diurnal colubrids and elapids such as *Coluber flagellum* and *Pseudonaja affinis,* which actively hunt their prey in hot arid and semi-arid environments, have relatively elevated PBTs falling between 32 and 34°C (e.g. *Salvadora exalepis,* Jacobson and Whitford 1971, *Pseudonaja textilis,* Witten 1969). The rest of the Colubroidea, regardless of whether they are species from temperate regions, which are invariably diurnal and heliothermic no matter what their mode of life, or species such as the desert vipers which move mainly at night and surprise their prey, have a PBT between 30 and 32.5°C (Cowles and Bogert 1944, Saint Girons and Saint Girons 1956, Witten 1969, Shine 1976, Spellerberg and Phelps 1975, Heatwole 1976, Saint Girons 1978). The temperature preference of the Natricinae living in temperate regions appear to be even lower with PBTs falling between 27 and 30°C (Stewart 1965, Kitchell 1969, Osgood 1970, Gehrmann 1971). The few data

published on snakes living in intertropical forests, most of which are not heliothermic, are difficult to interpret at this stage but it seems likely because of the high nocturnal temperatures characteristic of this environment that they also have low PBTs, as is the case with lizards inhabiting the same biotope (Ruibal and Philibosian 1970).

When they are preoccupied with activities such as food-seeking or courtship, heliothermic reptiles abandon to some extent their habitual precise thermoregulation. The minimum temperature voluntarily tolerated under these circumstances varies somewhat according to the type of activity in which the animal is engaged and can differ considerably from that measured for example at the beginning of the basking period. The maximum temperature voluntarily tolerated on the other hand appears to represent for the animal an upper physiological limit which cannot be exceeded, no matter what the activity. In temperate regions, exploratory behaviour or food-seeking is usually accompanied by a progressive fall in the body temperature to below the PBT whereas the reverse is the case with snakes living in hot arid regions which already have a PBT close to the upper limit of the normal activity range, and usually only a few degrees away from the maximum temperature voluntarily tolerated. This "overheating" during periods of more intense activity is particularly clear in the case of *Pseudonaja affinis* and, as a result, the mean body temperature of the snake during the sunny hours of the day was often as much as 1C° above the animal's PBT. It is possible that the rather high mean body temperature reported by Webb (1973, cited by Shine 1976) for the snake *Pseudonaja textilis* in an outdoor enclosure is due to the same phenomenon.

It is well established that European vipers, and probably the great majority of snakes, display thermal compensation when necessary. For example, during days with intermittent sunshine, vipers will manage to attain their PBT by a series of long basking periods in which they allow their body temperature to rise, almost to the maximum voluntarily tolerated, following periods of forced cooling when the sun is obscured by cloud (Saint Girons 1975). In hot regions this form of thermal compensation obviously functions in the opposite sense. Thus, after a period of exploration during which the body temperature of *Pseudonaja affinis* would rise to over 35°C, the snake would return to its shelter and allow its temperature to fall below 30°C before recommencing normal thermoregulation. It is also possible that this habitual exposure to elevated body temperatures permits arid-living species such as the dugite to retain a relatively low PBT, which is only of the order of 1 or 2C° higher than that of nocturnal species which lie in wait for their prey, despite their obvious thermophilia. This underlines the importance of knowing, in studies of comparative thermoregulation, not only the PBT, which is readily determined in a temperature gradient in the laboratory, but also the actual body temperatures to which the animals are exposed in the field.

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The distribution of benthic macroflora in the Swan River estuary, Western Australia

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Abstract

A survey of 53 of the most common benthic plants in the Swan River estuary shows the total number of species and their vertical distribution becomes smaller, while the proportion of chlorophycean species becomes larger, upstream from the mouth. Rapid and thorough freshwater flushing of the estuary in winter (June-August) results in a considerable decrease in species numbers and the survival of a few tolerant species, with rapid recolonization of the estuary when saline conditions return. The large number of algal species present suggests that pollution effects are low.

Introduction

In contrast with the estuaries of Europe and North America, the benthic macroflora of Australian estuaries has received very little ecological attention (Bayly 1975, Ducker, Brown and Calder 1977). In the case of the Swan River estuary, only brief species lists are provided by Thompson (1946) and Royce (1955). The recent book by Riggert (1978) provides an excellent account of the natural history of the Swan River estuary and contains a brief descriptive overview of the benthic flora.

This study provides data on seasonal, horizontal and vertical distribution of the macroflora as a baseline for future studies of changes in the flora of the Swan River estuary. The distribution of the Swan River estuary flora is compared with that of northern hemisphere estuaries, especially with a view to using the benthic plants as indices of pollution and other environmental disturbances.

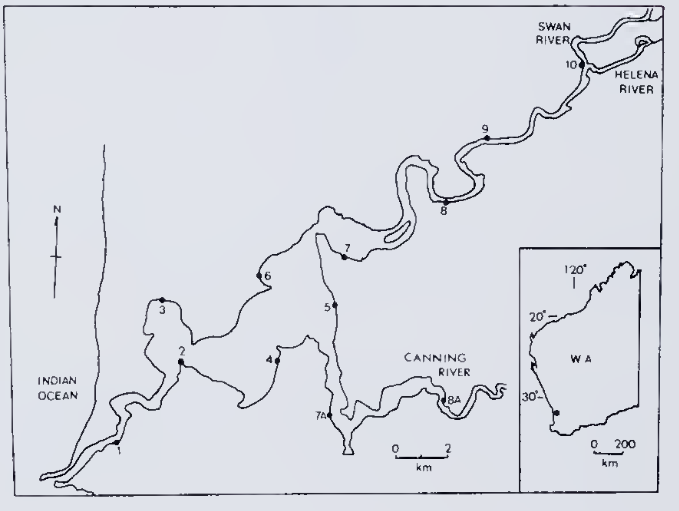

Figure 1.—Map of the Swan River estuary showing sampling stations.

Methods

The species of benthic multicellular plants of the estuary (including the diatom *Melosira moniliformis*) were collected as scrapings from all substrates (including sand, rock, wood, debris, shell fish) from the shoreline out to the limits of the photic zone at ten sites (Fig. 1) at 3-weekly intervals during 1968. The upper and lower depth limits of the plants were recorded, together with surface water temperatures (mercury thermometer) and salinities (conductivity meter). Tide level data were obtained from the Western Australian Public Works Department tide gauge near station 7 (Fig. 1), and from the Fremantle Port Authority gauge at the mouth of the estuary.

The upper limit of the study area was arbitrarily set at the junction of the Swan and Helena Rivers where the salinity was no greater than $5\,^{0}/_{00}$ and beyond which only 1-2 species of benthic algae occurred. The distribution of macroflora in the Canning River (stations 7A and 8A) was similar to that of the major arm of the estuary and will not be considered here.

Results

Hydrology

The hydrology of the Swan River estuary has been fully documented by Rochford (1951) and Spencer (1956). The seasonal phases of temperature and salinity were monitored during the study period to allow correlations with the distribution of the benthic flora. The summer-autumn phase was marine-dominated upstream to station 7 (Fig. 2), with salinity decreasing and water temperature increasing further upstream. After winter rainfall and fresh-

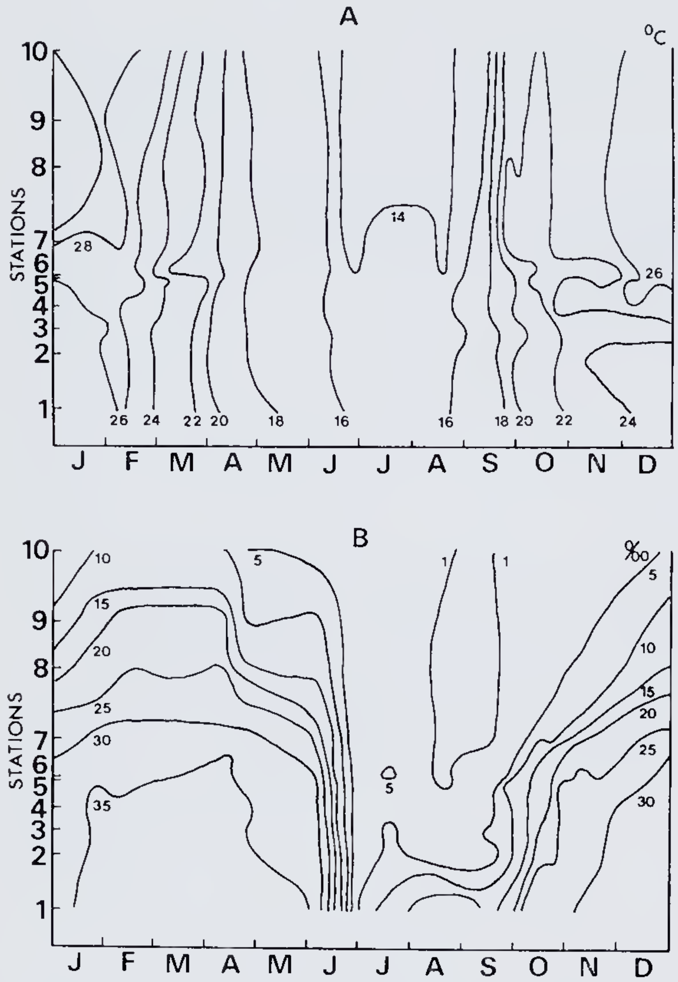

Figure 2.—Water temperature and salinity isopleths of the Swan River estuary. The stations are from Figure 1 and are scaled in distance upstream from the estuary mouth. A.—surface isotherms (°C), B.—surface isohalines (°/oo).

water runoff, the winter-spring phase had a halocline with cool freshwater to 2-5 m depth and high turbidity throughout the estuary. The tidal amplitude of about 0.9 m at the estuary mouth gradually decreased upstream. The average high tide level during December and January (summer) was 0.3-0.4 m lower than during June and July (winter) because of the lower mean sea level and considerably reduced river flow in summer.

Benthic Flora

Sixty-nine benthic species were identified in the Swan River estuary, of which four were angiosperms. The distribution of 53 of the most common species was used for the ecological analysis. The species of *Enteromorpha, Cladophora* and several Cyanophyta have not been reliably determined, and this is a world-wide problem (apart from some regional studies). These species, of which there are probably 2-4 per genus, are grouped under the generic name. A preliminary species list is provided in the Appendix and voucher specimens are deposited at the University of Western Australia.

The maximum (usually summer) horizontal distributions of the species are shown in Table 3. The proportions of Phaeophyta and Rhodophyta to Chlorophyta species became smaller with increasing distance from the mouth of the estuary. The reduction in the total number of species upstream was highly correlated with surface salinity conditions (Table 1). During the late winter freshwater months, few species occurred throughout the estuary. The seasonal distributions of algae in the estuary (for example stations 1-3, Table 4) show that most species were annuals and that the time of reappearance of each species varied. The proportion of perennial to annual species increased upstream, and the same perennial species occurred throughout the estuary. The vertical distribution limits of the attached macroalgae decreased upstream (Table 2). The total vertical range was least in winter (July) with both the upper and lower vertical limits generally higher than in summer (January). Most species occurred on solid substrates (rock, wood, concrete), and many were also epiphytic. Eight species (Table 3) were found free-floating as well as attached. *Gracilaria verrucosa,* in particular, often occurred unattached and deeper than other attached algae.

Discussion

The overall distributional features of the macroflora of the Swan River estuary are in general agreement with previous northern hemisphere studies

Table 1

The number of benthic plant species in the Swan River estuary throughout the year, correlated with the salinity distribution for each month. The stations are shown in Figure 1.

Stations	Months											
	J	F	M	A	M	J	J	A	S	O	N	D
10	1	1	2	1	4	2	3	0	1	3	2	1
9	2	1	4	5	3	4	2	0	2	2	3	1
8	4	3	4	5	6	3	2	5	2	4	5	4
7	9	6	9	10	8	5	5	6	7	8	6	5
6	7	7	11	6	9	6	5	9	5	5	8	8
5	9	10	15	15	10	14	10	11	7	11	7	7
4	11	4	8	10	10	9	9	6	4	8	8	8
3	17	19	21	21	18	14	17	11	12	13	14	13
2	13	11	20	21	18	15	14	11	9	9	13	12
1	16	18	24	24	20	22	24	10	9	10	17	15
r	0·87	0·70	0·76	0·73	0·81	0·94	0·88	0·39	0·63	0·82	0·84	0·87

Table 2

The upper and lower vertical limits of macroalgae throaghoat the Swan River estaary in January (summer) and Jaly (winter). Figures are in cm, relative to mean sea level at Fremantle, Western Aastralia. The station nambers are shown in Figure 1.

	Stations	1	2	3	4	5	6	7	8	9	10
January	upper limit	+67	+70	+61	+58	+67	+73	+61	+40	+67	+67
	lower limit	−198	−46	−335	−61	−76	+27	+15	+15	+18	43
July	upper limit	+101	+91	+98	+79	+76	+73	+94	+70	+64	+70
	lower limit	−259	+12	−198	−15	−70	+46	+9	+64	+52	+64

Table 3

The maximum horizontal distribation of 53 selected benthic plants in the Swan River estuary, independent of the time of the year. The stations are shown in Figure 1. (*) denotes species occurring both free-floating and attached.

Species	Stations 0	1	2	3	4	5	6	7	8	9	10
Calothrix crustacea	=	=									
Rhizoclonium hookeri	=	=									
Bryopsis plumosa	=	=									
Porphyra lucasii	=	=									
Champia parvula	=	=									
Laurencia sp.	=	=									
Chondria dasyphylla?	=	=									
Spyridia filamentosa	=	=									
Melobesia membranacea	=	=									
Spirulina subtilissima	=	=	=								
Acetabularia calyculus	=	=	=								
Sphacelaria tribaloides	=	=	=								
Hypnea cervicornis	=	=	=								
Codium harveyi	=	=	=	=							
Cladophoropsis herpestica	=	=	=	=							
Oscillatoria spp.		=	=	=							
Dictyota dichotoma	=	=	=	=							
Calpomenia peregrina	=	=	=	=							
Bangia fuscoparparea	=	=	=	=							
Gelidiam pusillum	=	=	=	=							
Cystoseira trinodis		=	=	=							
Hormophysa triqaetra			=	=	=						
Grateloupia filicina	=	=	=	=	=						
Monospora australis	=	=	=	=	=						
Chaetomorpha area	=	=	=	=	=	=					
**Chaetomorpha linum*	=	=	=	=	=	=					
Ulva lactuca	=	=	=	=	=	=					
Sphacelaria furcigera	=	=	=	=	=	=					
Chondria tenuissima	=	=	=	=	=	=					
Chondria sp.	=	=	=	=	=	=					
**Ceramium cliftonianum*	=	=	=	=	=	=					
Rosenvingea orientalis	=	=	=	=	=	=	=				
Giffordia irregalaris	=	=	=	=	=	=	=				
Goniotrichum alsidii	=	=	=	=	=	=	=				
Ulothrix subflaccida	=	=	=	=	=	=	=				
Callithamnion pasillum?	=	=	=	=	=	=	=				
Microcoleus acutissimus		=	=	=	=	=	=	=			
Polysiphonia subtilissima	=	=	=	=	=	=	=	=			
Giffordia mitchellae	=	=	=	=	=	=	=	=			
Calothrix spp.		=	=	=	=	=	=	=	=		
Cladophora spp.	=	=	=	=	=	=	=	=	=		
Audoainella thuretii	=	=	=	=	=	=	=	=	=		
Ulvaria oxysperma	=	=	=	=	=	=	=	=	=	=	
**Enteromorpha* spp.	=	=	=	=	=	=	=	=	=	=	
**Ectocarpus silicalosas*	=	=	=	=	=	=	=	=	=	=	
**Gracilaria verrucosa*	=	=	=	=	=	=	=	=	=	=	
**Rhizoclonian riparium*	=	=	=	=	=	=	=	=	=	=	=
**Melosira moniliformis*	=	=	=	=	=	=	=	=	=	=	=
**Vaucheria* sp.			=	=	=	=	=	=	=	=	=
Lyngbya latea		=	=	=	=	=	=	=	=	=	=
Zostera macronata	=	=									
Halophila ovalis	=	=	=	=	=	=					
Potamogeton pectinatus										=	=

Table 4

The seasonal distribution of benthic plants in the lower Swan River estuary (stations 1–3 in Figure 1).

Species	J	F	M	A	M	J	J	A	S	O	N	D
	Months											
Codium harveyi		=	=									
Vaucheria sp.									=			
Lyngbya lutea							=					
Spirulina subtilissima							=					
Chondria sp.						=	=					
Microcoleus actissimus							=	=	=			
Ulvaria oxysperma						=	=	=	=			
Porphyra lucasii					=	=	=		=			
Cladophoropsis herpestica			=	=			=	=	=			
Melobesia membranacea			=	=	=	=	=					
Bangia fuscopurpurea			=	=	=	=	=					
Bryopsis plumosa			=	=		=						
Spyridia filamentosa			=				=					
Calothrix spp.				=		=	=					
Goniotrichum alsidii			=	=	=	=	=					
Ceramium cliftonianum	=	=	=	=	=	=						
Chondria tenuissima	=	=	=	=	=	=						
Laurencia sp.	=		=	=			=					
Ulothrix subflaccida	=	=	=	=	=	=	=					
Rosenvingea orientalis	=	=	=	=							=	=
Cystoseira trinodis	=	=	=	=	=						=	=
Hypnea cervicornis	=	=	=	=	=	=						
Oscillatoria spp.				=			=					=
Giffordia spp.		=	=	=	=	=	=					=
Champia parvula?	=		=	=		=					=	
Monospora australis	=	=		=			=			=	=	
Dictyota dichotoma	=	=	=	=	=	=					=	=
Polysiphonia subtilissima	=	=	=	=	=	=			=	=	=	=
Sphacelaria spp.	=	=	=	=	=		=			=	=	=
Colpomenia peregrina	=	=	=	=	=	=	=			=	=	=
Chaetomorpha spp.	=	=	=	=	=	=	=	=		=		=
Melosira moniliformis		=	=	=	=	=	=	=	=	=	=	=
Callithamnion pusillum?	=	=	=	=	=	=	=	=	=	=	=	
Ulva lactuca	=	=	=	=	=	=	=	=	=	=	=	=
Grateloupia filicina	=	=	=	=	=	=	=	=	=	=	=	=
Enteromorpha spp.	=	=	=	=	=	=	=	=	=	=	=	=
Rhizoclonium riparium	=	=	=	=	=	=	=	=	=	=	=	=
Gelidium pusillum	=	=	=	=	=	=	=	=	=	=	=	=
Gracilaria verrucosa	=	=	=	=	=	=	=	=	=	=	=	=
Ectocarpus siliculosus	=	=	=	=	=	=	=	=	=	=	=	=
Audouinella thuretii	=	=	=	=	=	=	=	=	=	=	=	=
Cladophora spp.	=	=	=	=	=	=	=	=	=	=	=	=
Halophila ovalis	=	=	=	=	=	=	=	=	=	=	=	=

(e.g. Conover 1958, den Hartog 1967, Mathieson and Fralick 1972, 1973, Kjeldsen and Phinney 1971), in that there are fewer and fewer species of essentially marine algae penetrating upstream from the estuary mouth. A causal relationship between species presence and salinity distribution in estuarine environments is supported by experimental evidence for the deleterious effects of freshwater upon the growth and metabolism of macroalgae (e.g. Gessner and Schramm 1971, Kjeldsen and Phinney 1971).

The marked two-phase hydrology of the Swan River estuary is reflected in the sudden winter decrease in the number of algal species and their populations in the estuary, an effect attributed to the rapid flushing of the estuary with cool, turbid freshwater from the Swan, Helena and Canning Rivers. Although a halocline persists through winter with saline water at depths greater than 2·5 m almost all the benthic flora is shallow water and within the freshwater zone (Table 2).

The seasonal reduction in species diversity in the Swan River estuary is not a feature of the northern hemisphere estuaries mentioned above. Consequently, the flora of the Swan River estuary may be categorized into either annual or perennial groups depending upon whether the plants survive the winter season. However some species (e.g. *Enteromorpha* spp. and *Cladophora* spp.) do not conveniently fit into either category as they are continuously represented by successive generations (the seasonal annual concept of Sears and Wilce 1975). There is the additional consideration of physiological races of species adapted to different conditions within the same estuary (Bolton 1977). These mechanisms of rapid population turnover and adaptation must increase the tolerance and distributional limits of some estuarine species. Most annual and perennial species repopulate rapidly with the return of saline conditions in summer. However variations in times of reappearance of the annual species suggests that there are differences in physiology or over-wintering strategy. For example, regrowth from persistent fragments may be faster than growth from spores.

The vertical distribution of estuarine algae has received little attention apart from that observed in the intertidal zone (den Hartog 1967) and in brackish water submergence in fjords (Gessner and Schramm 1971). In the Swan River estuary the reduced vertical ranges of attached macroalgae upstream and during the freshwater phase (Table 2) may be because the deep water species (e.g. *Monospora australis*, *Gelidium pusillum* and *Polysiphonia subtilissima*) cannot tolerate continuous exposure to low salinities, although increased turbidity in winter also may be involved.

The number of benthic species in estuaries apparently depends upon the penetration and duration of marine water in the estuaries. Estuaries with more than 70 algal species, for example Great Pond, Massachusetts (Conover 1958) and Great Bay, New Hampshire (Mathieson and Fralick 1972) are strongly marine influenced for most of the year. The Swan River estuary is probably in this category despite the severe freshwater influence of winter. Estuaries with a large freshwater influence or those affected by pollution contain fewer (about 30) species (Edwards 1972, Mathieson and Fralick 1973). With at least 65 species of benthic algae in the Swan River estuary, the system shows no evidence of pollution effects.

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Appendix

A preliminary list of benthic marine algae and seagrasses in the Swan River estuary. The main reference used in identification are also given.

Cyanophyta

Calothrix confervicola (Roth) C. Agardh? Fan 1956. Chapman 1956.
Calothrix crustacea Thuret Fan 1956. Chapman 1956.
Calothrix sp.
Lyngbya lutea (C. Agardh) Gomont Chapman 1956. Desikachary 1959.
Microcoleus acutissimus Gardner Chapman 1956. Desikachary 1959.
Oscillatoria amphibia C. Agardh Desikachary 1959.
Oscillatoria sp. 1.
Oscillatoria sp. 2.
Spirulina subtilissima Kuetzing Chapman 1956. Desikachary 1959.

Chlorophyta

Acetabularia calyculus Quoy et Gaimard Solms-Laubach 1895.
Bryopsis plumosa (Hudson) C. Agardh Chapman 1956.
Caulerpa racemosa (Forsskal) J. Agardh var. *laetevirens* Montagne) Wever van Bosse Cribb 1958.
Chaetomorpha aerea (Dillwyn) Kuetzing Chapman 1956.
Chaetomorpha linum (Mueller) Kuetzing Chapman 1956.
Cladophora albida (Hudson) Kuetzing? Soderstrom 1963.
Cladophora fascicularis (Mertens in C. Ag.) Kuetzing? Soderstrom 1963.
Cladophora flexuosa (Mueller) Kuetzing? Soderstrom 1963.
Cladophora harvey Womersley? Womersley 1956.
Cladophora laetevirens (Dillwyn) Kuetzing? Soderstrom 1963.
Cladophora sp.
Cladophoropsis herpestica (Montagne) Howe Cribb 1960.
Codium harveyi Silva Silva and Womersley 1956.
Enteromorpha ahlneriana Bliding? Bliding 1963.
Enteromorpha compressa (Linnaeus) Greville Bliding 1963.
Enteromorpha flexuosa (Wulfen ex Roth) J. Agardh? Bliding 1963.
Enteromorpha sp.
Rhizoclonium hookeri Kuetzing? Chapman 1956.
Rhizoclonium riparium (Roth) Harvey Chapman 1956. Bliding 1957.
Ulothrix subflaccida Wille Ramanathan 1964.
Ulothrix sp.
Ulva lactuca Linnaeus Chapman 1956.
Ulvaria oxysperma (Kuetzing) Bliding var. *oxysperma* Bliding 1968.

Phaeophyta

Colpomenia peregrina (Savageau) Hamel Clayton 1975.
Cystoseira trinodis (Forsskal) C. Agardh Papenfuss and Jensen 1967.
Dictyota dichotoma (Hudson) Lamouroux Lindauer Chapman and Aiken 1961.
Ectocarpus siliculosus (Dillwyn) Lyngbye Clayton 1974.
Giffordia mitchellae (Harvey) Hamel Clayton 1974.
Giffordia irregularis (Kuetzing) Joly Clayton 1974.
Hormophysa triquetra (C. Agardh) Kuetzing Papenfuss 1967.
Rosenvingea orientalis (J. Agardh) Boergesen Misra 1966.
Sphacelaria furcigera Kuetzing Misra 1966.
Sphacelaria tribuloides Meneghini Misra 1966.

Chrysophyta

Melosira moniliformis (Mueller) C. Agardh Cupp 1943.

Xanthophyta

Vaucheria sp.

Rhodophyta

Audouinella thuretii (Bornet) Woelkerling Woelkerling 1971.
Bangia fuscopurpurea (Dillwyn) Lyngbye Levring 1953.
Callithamnion pusillum Harvey? Harvey 1855.
Ceramium cliftonianum J. Agardh Womersley 1978.
Champia parvula (C. Agardh) Harvey Reedman and Womersley 1976.
Chondria dasyphylla (Woodward) C. Agardh? Harvey 1855.
Chondria tenuissima (Goodenough & Woodward) C. Agardh Lucas and Perrin 1947.
Chondria sp.
Monospora australis (Harvey) J. Agardh Baldock 1976.
Gelidium pusillum (Stackhouse) Le Jolis Chapman 1969.
Goniotrichum alsidii (Zanardini) Howe Levring 1953.
Gracilaria verrucosa (Hudson) Papenfuss May 1948.
Grateloupia filicina (Wulfen) C. Agardh Lucas and Perrin 1947.
Griffithsia crassiuscula C. Agardh Baldock 1976.
Hypnea cervicornis J. Agardh Taylor 1960.
Laurencia sp.
Melobesia membranaceae (Esper) Lamouroux? Dawson 1960.
Polysiphonia subtilissima Montagne Womersley 1979.
Porphyra lucasii Levring Womersley and Conway 1975.
Spyridia filamentosa (Wulfen) Harvey Womersley and Cartledge 1975.

Anthophyta

Halophila ovalis (R. Brown) Hooker den Hartog 1970.
Heterozostera tasmanica den Hartog den Hartog 1970.
Potamogeton pectinatus Linnaeus Smith and Marchant 1961.
Zostera mucronata den Hartog den Hartog 1970.

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Fish scales from the Permian of Western Australia

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Abstract

Fish scales are recorded for the first time from the Permian of Western Australia. The scales, from the Byro Group in the Carnarvon Basin, are distinct from any Permian fish scales previously described from the Gondwanaland continents. The fish may have inhabited an open marine environment.

Introduction

Remains of fish are sporadic in the Permian deposits of the Gondwanaland continents. The present note documents the recent discovery of fish scales from the Coyrie Formation, Byro Group, of the Carnarvon Basin, Western Australia. These fish scales, collected during the recent mapping of the Carnarvon Basin by the Geological Survey of Western Australia (GSWA) (see Hocking *et al.* 1980 for revised stratigraphic nomenclature) are noteworthy because of their mode of occurrence, size and the environment of deposition.

Australian Permian fish

Few fish have been recorded from the Permian strata of Australia. The Sydney Basin (eastern Australia) has yielded the genus *Urosthenes* Dana (1848a, p.433; 1848b, p.149; 1849, p.171, Atlas Pl. 1 fig. 1-1a) with the type species *U. australis* Dana from the Newcastle Coal Measures and *U. latus* Woodward (1931) from the same strata. Woodward (1940) subsequently described a representative of *Elonichthys* from the same strata. The report by de Koninck (1877, p.354) of the bradyodont shark *Tomodus convexus* Agassiz? from New South Wales cannot be confirmed as the specimens were destroyed by fire (Teichert 1943, p.543-4). *Urosthenes* Dana lived in a non-marine habitat whereas de Koninck's bradyodont shark was probably of marine origin. Fossil fish remains have also been recorded from the Bowen Basin of Queensland by Dunstan (1901). The Queensland material included spines, vertebrae and scales; however, the specimens have apparently never been described or figured.

Records of fish in the Western Australian Permian Basins are restricted, to date, to several reports from the Carnarvon Basin. *Helicoprion* Karpinsky has been described from the Wandagee Formation (Woodward, 1886; Teichert, 1940) as well as representatives of bradyodont sharks (*Helodus* Agassiz and *Crassidonta* Branson) from the same formation (Teichert, 1943). The Wandagee Formation possesses a diverse invertebrate fauna, including articulate brachiopods, molluscs and crinoids, indicative of an open marine environment. *Helicoprion* has also been recorded from the Bulgadoo Shale (Condon, 1967) a formation also with a diverse marine invertebrate fauna.

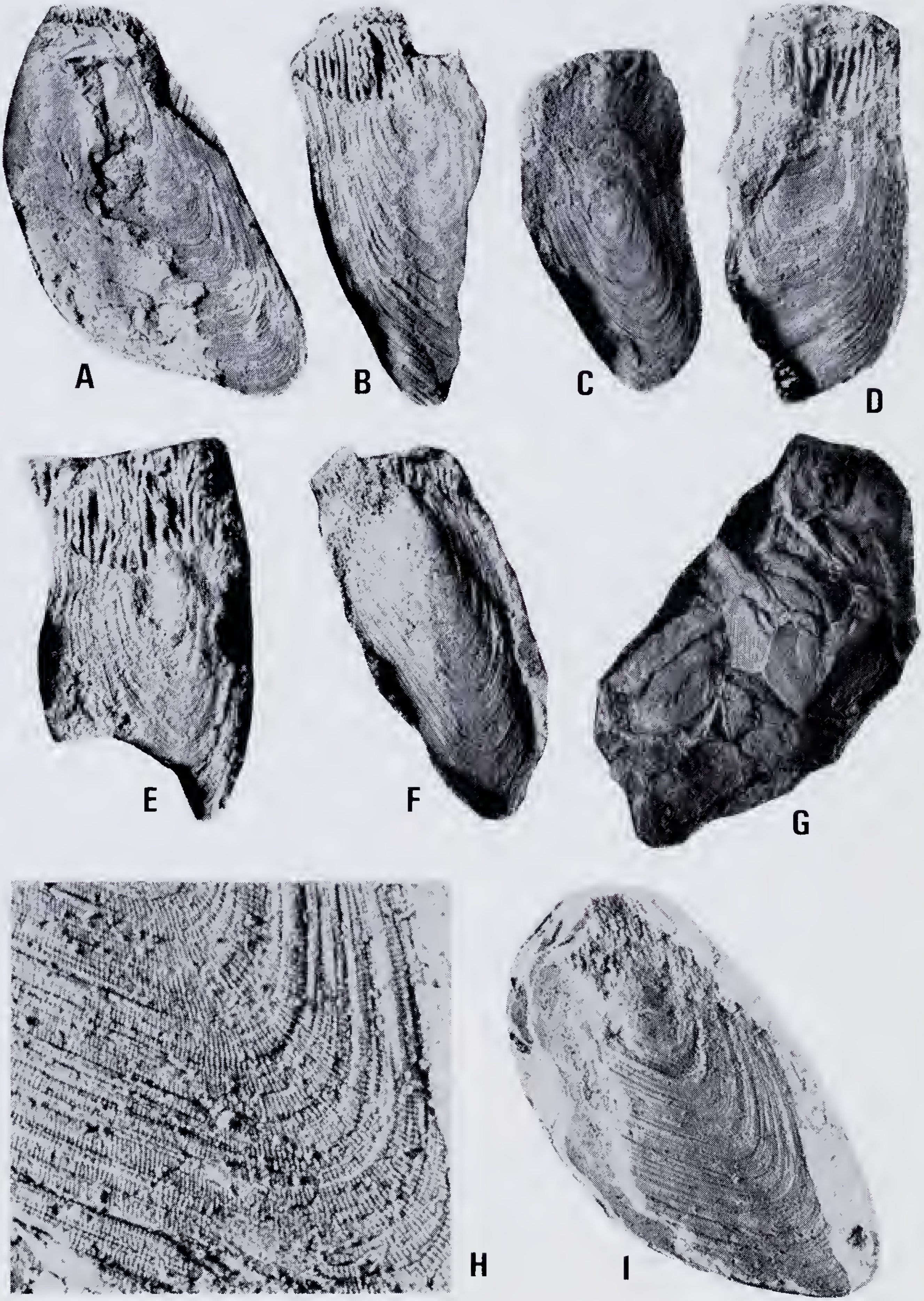
The new discovery

In addition to the fish scales, GSWA sample 44553 (Lat. 25°49′28″ S, Long. 115°38′33″E, about 300 m south of Wooramel River, north-east of Darcy Hill; near top of Coyrie Formation) has yielded abundant, although invariably poorly preserved, specimens of *Fusispirifer byroensis* (Glauert 1912). Glauert's species is diagnostic of the Coyrie Formation and the Mallens Sandstone. Three specimens of *Fusispirifer byroensis* from sample 44553 have been registered in the GSWA collection with the numbers F11014, F11015, F11016. The age of these stratigraphic units is well controlled and is considered to be early Permian (Late Artinskian Stage, Early Baigendzinian Substage, Dickins 1976).

The discovery of fish scales from the same locality as abundant articulate brachiopods is of considerable interest because of the indubitably marine environment of deposition. The fish scales, described below, are large, ranging in length from 1 cm to 1.7 cm. The scales, well over one hundred specimens, are preserved in a single block of rock some 12 cm x 8 cm in size. The scales are thickly distributed, in random orientation throughout the block, with no indication of bedding or sedimentary structures. Such an aggregate of scales is suggestive of coprolitic accumulation, although no discrete coprolite shape was observable. Breaking the block revealed further scales throughout the entire specimen. The block is ferruginised with some original, though decomposed, material of the scales remaining with the impressions of the scales. If the block is coprolitic its size indicates a large predatory organism.

Affinities of the scales

In an attempt to identify the scales a survey of Permian fish occurrences of the Gondwanaland continents was made. Few described fish scales were found to be similar, probably because of the inade-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quate documentation and illustrations of many reports. For the present, the nomenclature of the scales is left open, although it appear likely that the scales are of palaeoniscid affinity.

Permian fish scales have been recorded from Southern Africa, South America and India. However despite the substantial records the only fish scales from Southern Africa comparable to the present specimens from Western Australia, with respect to their apparent concentric ornament and strongly digitate hind margin, are the flank fish scales of *Acrolepis molyneuxi* figured by Woodward (1903, 1910). The South African fish scales are much smaller than the new Western Australian specimens.

The records of fish scales from the Late Palaeozoic of South America are plentiful, however, descriptions and illustrations are few. Fish scales described and figured by Martins (1948) are closely comparable with the new material especially in details of ornament and the digitate hind margin. Martins' specimens, from the Serie Marica, Rio Grande do Sol, are, however, smaller and possess a coarser concentric ornament than the Western Australian scales. Associated with the fish scales, Martins recorded an impoverished marine fauna of inarticulate brachiopods (*Lingula* and *Orbiculoidea*) indicative of marginal marine deposits.

Environment of the Western Australian scales

The determination of the environment of deposition of fossil fish is of critical importance and requires careful examination of stratigraphic evidence. Romer (1971, p.120) has commented on the uncertainty of habitat of many of the described forms, and on the problem of euryhaline species as well as those species with differences between early and late life stages. As noted above the Western Australian scales occur in sediments deposited in an open marine environment. Nevertheless caution about the habitat of the Western Australian fish is advisable, because of the inferred coprolite source of the specimens.

Systematic Palaeontology

Class PISCES

Incertae Sedis.

Description: The scales (Fig. 1) are of varying shape and outline, reflecting the varying position of the scales on the body of the fish. Length of the scales varies from 1 cm to 1.7 cm. The hind margin of the scales is digitate in an anastomosing pattern. The digitate portion of the scale is up to one quarter of the total length of the scale. The scales are thick (up to 0.5 mm) with one surface being smooth (the inner surface?), while the other surface possesses an ornament of sub-concentric lines and a micro-ornament of striae which increase in number anteriorly by intercalation. On worn impressions of scales this micro-ornament is lost.

Discussion: The thickness of the scales and the micro-ornament make these scales distinct from any record elsewhere from the Permian. The scales described by Martins (1948) discussed above are impressions that are possibly too worn (or the lithology may be too coarse) to preserve any micro-ornament. Close comparison was indicated with scales figured by Martins; however, as these were left in open nomenclature little can be added except that both the South American and Western Australian forms are distinct and possibly represent at least one new genus likely to be of palaeoniscid affinity.

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Figure 1.—Fish scales from GSWA sample 44553. All specimens whitened with ammonium chloride. A.—GSWA F11006 fish scale x 5. B.—GSWA F11007 fish scale x 5. C.—GSWA F11008 fish scale x 5. D.—GSWA F11009 fish scale x 4.5. E.—GSWA F11010 fish scale x 5. F.—GSWA F11011 fish scale x 5. G.—GSWA F11016 portion of block with fish scales x 1, H.—GSWA F11012 portion of fish scale x 12. I.—GSWA F11012 fish scale x 5.

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Observations on the breeding biology and behaviour of the long-necked tortoise, *Chelodina oblonga*

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Abstract

Chelodina oblonga, a common tortoise in the fresh waters of the south-western coastal belt of Western Australia, has two nesting periods: one in spring (September to November), and one in summer (December to January). Cool conditions with rain occur during the spring period, and hot dry conditions prevail during the summer period. Specific weather conditions were associated with the nesting periods including the occurrence of seasonal rain-bearing low pressure systems, a falling barometric pressure, and an air temperature above 17°C. Distances travelled by the gravid female to the nesting site were variable and were generally greater during the spring period. Animals were active within a body temperature of 18°C to 31°C and dehydrated quickly with air temperatures in excess of 25°C. Difference in clutch sizes were apparent between nesting periods, and egg weights, egg sizes and clutch sizes varied between individuals. The incubation period was almost identical for each nesting period, ranging from 210 days to 222 days. Hatchlings from both nesting periods emerged at the same time in mid-August.

Introduction

The family Chelidae is represented in Western Australia by six species of fresh-water tortoise. *Chelodina rugosa* is found only in the Kimberley and *C. steindachneri* is found in the arid zone within the river systems from the Irwin River south of Geraldton to the De Grey River in the Pilbara. The short-necked tortoises are represented by *Emydura australis* and *Elseya dentata* in the Kimberley, and *Pseudemydura umbrina* which occupies an area of a few square kilometres just north-east of Perth. The common long-necked tortoise, *Chelodina oblonga,* is found in the south-west of Western Australia (Cogger 1975).

Although *C. oblonga* is common in the south-west of Western Australia there is little literature available concerning its behaviour in the field. Burbidge (1967) investigated the biology of *Pseudemydura umbrina* and *Chelodina oblonga.* Nicholson (1974 pers. comm.) described the nesting behaviour of *C. oblonga.*

The aim of this paper is to report on the movements and breeding behaviour of a wild population of *C. oblonga.* Over a period of four years climatic and seasonal factors which are associated with movement and reproductive biology have been measured and an attempt was made to assess those environmental variables which affect breeding.

Study area

Thompson Lake Nature Reserve No. 15556, vested in the Western Australian Wildlife Authority and managed by the Department of Fisheries & Wildlife, and the Marsupial Breeding Station, No. 29241

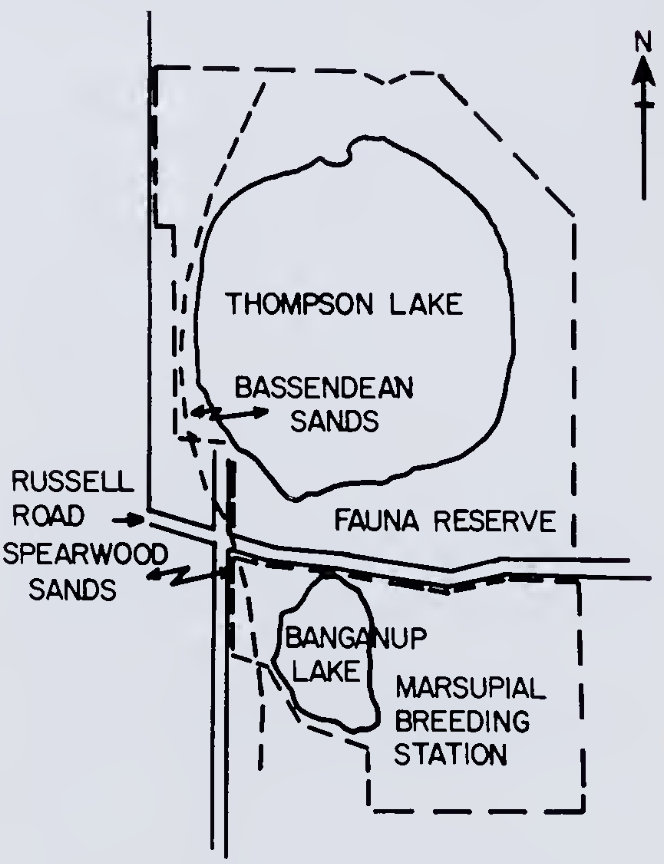

Figure 1.—Map showing study areas and boundary between the Bassendean-Spearwood Sands; scale: 1:25 000.

managed by the University of Western Australia and vested in the Minister for Fisheries and Wildlife are both situated in the City of Cockburn. These study areas lie approximately 25 km south of Perth, Western Australia at latitude 32° 10′ S, longitude 115° 50′ E. The total area of Thompson Lake Reserve is 509 ha with the lake occupying 172 ha. The area of the Marsupial Breeding Station is 253.7 ha with Banganup Lake occupying 32 ha (Fig. 1).

The two reserves lie mostly within the Bassendean Sand complex with the Spearwood Sands bordering Thompson and Banganup Lakes on their west side (Seddon 1972). The boundary between the two sands is shown in Figure 1.

The vegetation of the higher well-drained Bassendean Sands consists mainly of Jarrah *(Eucalyptus marginata)* and *Banksia* spp. The vegetation on the higher Spearwood Sands consists mainly of *Banksia* spp, Jarrah and Tuart (*Eucalyptus gomphocephala*). The lower areas close to the lakes are dominated by the Swamp Gum (*E. rudis*), paperbarks (*Melaleuca* spp.) and the jointed rush *Baumea articulata* in varied associations with other reeds and rushes.

Methods and materials

Capture

Animals moving to nest were captured on the boundary fence surrounding the Marsupial Breeding Station. Females in the Thompson Lake Reserve were captured as they moved to nest and other females were followed to the nest site. Animals were also captured in simple wire mesh fish type traps using liver as bait.

Marking and measurement

Where possible adults were weighed on a Salter spring balance, weighing to the nearest gm. Carapace and plastron widths and lengths, body depths and tail lengths were measured, the last from the tip of the tail to the middle of the concave section of the plastron with linear calipers. Stainless steel tags were inserted in two holes drilled on the edge at the rear of the carapace. Because the metal tag disintegrates, the same number was also branded on the middle of the plastron using a cauterizer. The presence of eggs was determined by pushing the index finger against the abdominal cavity.

Distances from the water's edge to the nest site were measured during the two nesting periods. Nest sites were located by regular and systematic searching of the study areas. Some nest sites were left undisturbed, marked with a wooden stake and labelled. Each nest site was surrounded with wire mesh and fly wire attached to the lower half to prevent hatchlings from escaping. Other nest sites were excavated and measured, and the eggs removed for other experiments. Eggs were measured with linear calipers and weighed on a Mettler P 1200 balance.

Artificial nest sites similar to the original sites were selected and egg chambers dug by hand. Times from nesting to the emergence were recorded. Other eggs were placed in glass-fronted nest chambers to observe hatching and emergence dates.

Body, water and nest temperatures were recorded with a YSI model 44 telethermometer.

Weather

Rainfall figures were monitored daily at the Marsupial Breeding Station throughout the study period. High and low pressure systems were followed by studying the daily weather charts published by the Western Australian Bureau of Meteorology. Temperature and relative humidity were recorded continuously on a Thiess hygrothermograph maintained in a Stevenson Screen.

Results

Mating

Although intensive observations were made daily throughout the nesting periods, *C. oblonga* were never observed copulating on land or in the water.

Sex determination

Gravid females were easily sexed. Post mortems were carried out to determine the sex of non-gravid females and suspected males and from these data all tortoises were sexed from the ratio of the tail length to the body depth. Females have a ratio of less than 1.0 : 1 and the males a ratio greater than 1.4 : 1 (Fig. 2). The difference between females and males is highly significant ($p < .001$).

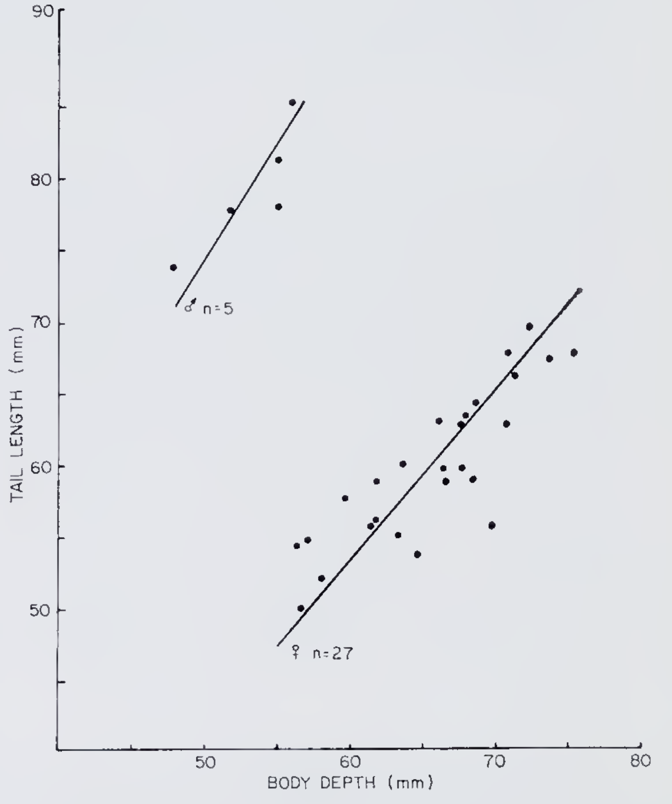

Figure 2.—Ratio of tail length to body depth of male and female *Chelodina oblonga* is highly significant ($.01 < P < .001$).

Nesting periods

Weather.—In south-western Australia the highest rainfall occurs during the winter months (Western Australian Year Book 1973). From observations during this study tortoises moved to nest for the laying of the first clutch of eggs at the end of

winter. The earliest movement was recorded on 9 September 1974 and the latest movement was recorded at the beginning of November 1976. The second nesting period did not correlate with any observed weather pattern.

Stimulus for movement.—During this study the lowest recorded body temperature was 18°C with an air temperature of 16.2°C at the time of capture. The highest recorded body temperature was 31.0°C with an air temperature of 27.0°C at time of capture (Fig. 3). Once the maximum daily temperature remains above 17.5°C the females move to nest (Fig. 4). Mean daily maximum temperature on days of movement during the summer period are higher than those during the spring period (Table 1).

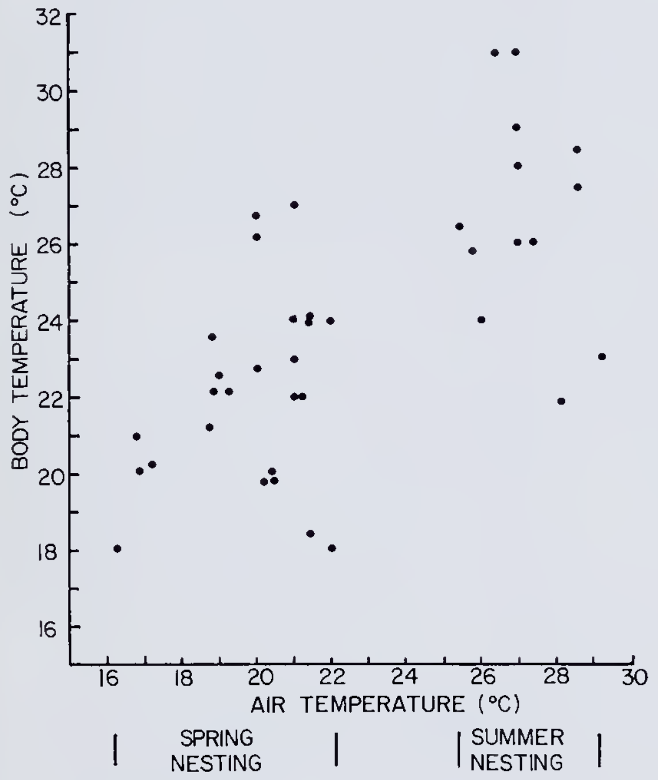

Figure 3.—Body and air temperatures at time of capture of gravid females moving to nest during the spring and summer nesting periods.

Weather patterns during the spring period characteristically approach from the south-west, and associated low pressure systems are normally rain-bearing depressions. Records during this study indicate that the females move to nest as the barometric pressure decreases (Fig. 5). A strong relationship between animal movement and the approach of a rain-bearing depression is evident. Barometric patterns typical of those correlated with movements of females are shown in Figure 5. Once the spring nesting period has commenced, future spring nesting periods may be predicted by observation of the weather patterns. There is no relationship between the weather pattern and the movement of the second nesting.

Movement.—During this study most animals captured were females moving to nest. The 1975/1976 data show that of the 76 animals captured, 67 were females and 9 were males. Of the 67 females

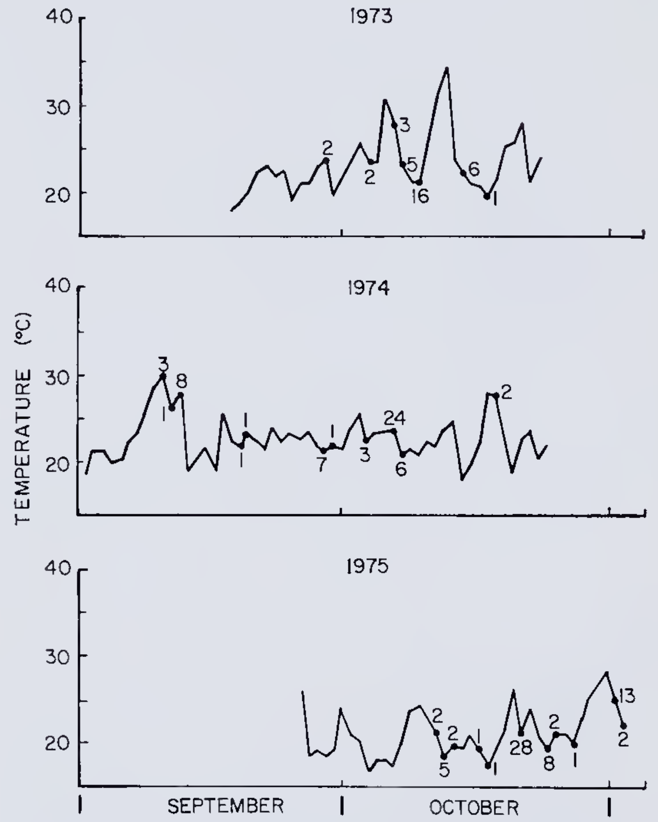

Figure 4.—Females moving to nest after daily maximum temperatures remain above 17.5°C and showing numbers with daily maximum temperatures.

Table 1

Mean daily maximum temperature (°C) recorded on day of movement

Movement	Mean daily maximum temperature on day of movement	Number of days on which movements were observed
Sept./Nov.		
1973	24·0	7
1974	23·5	13
1975	20·6	11
Dec./Jan.		
1973/74	32·1	11
1974/75	25·9	3
1975/76	26·7	6

captured 12 animals were without eggs and it was presumed that these had already laid eggs (Table 2). It is evident that females move to nest during both September/November and December/January. Males appear to move both prior to and after the main nesting periods (Table 2).

There was no evidence to show that females migrate except where the natural environment is drying up. Females during this study appeared to move only to nest. Males captured appeared to be migrating from one lake to the next.

Nesting and nest site

Approach to shore.—*C. oblonga* approached the shore very cautiously. Remaining in shallow water with the head held well above the water line and

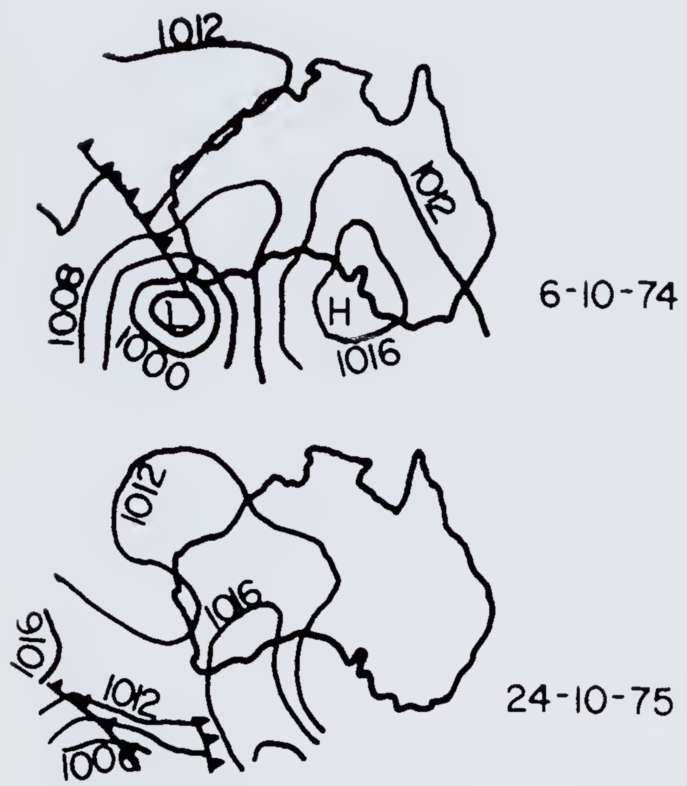

Figure 5.—Isobars recorded by the Weather Bureau at 1500 h indicating approaching cold fronts. 24 gravid females were captured moving to nest on the 6/10/74 whereas no animals were captured on the 24/10/75. 15 gravid females were captured 25th-26th as the depression with falling pressure moved over the coast.

Table 2

Male and female movement during the periods (*a*) 1975/1976 *and* (*b*) 1976/1977

(a)

Date	Female	Male
Sept. 1975	0	2
Oct. 1975	62	2
Nov. 1975	3	2
Jan. 1976....	2	2
Feb. 1976	0	1
	*67	9

* 12 females without eggs.

(b)

Date	Female	Male
Sept. 1976	1	1
Oct. 1976	1	5
Nov. 1976	13	1
Dec. 1976	1	0
Jan. 1977....	4	0
	20	7

at the same time resting on the lake bed, animals would take varying lengths of time before emerging. At this stage they were easily disturbed and would retreat to deeper water. As observed by Hendrickson (1958) *Chelonia mydas* approaches the shore in the same way.

Order of events during nesting.—Typical nesting behaviour of *C. oblonga* taken from field note book dated 6 October 1974:

0945 h Proceeded to study area at Thompson Lake. A rain-bearing low depression forecast. Air temperature 22°C with a light south-westerly wind and 8/10 cloud cover.

0955 h Observed female tortoise leaving the water. During the first 40 m the tortoise did not deviate from its original course, in a south-westerly direction. Once it gained the protection of the vegetation it used all available cover.

1050 h Started to move in a southerly direction.

1112 h Selected nest site. The site was open and comparatively flat with little vegetation except for native grasses. The nest site was 98 m from the water's edge. The tortoise began digging the nest chamber. Digging the vertical shaft was a simple process, with the tortoise using the rear feet alternately to scoop the soil out and place the material to one side of the hole. Construction of the egg chamber was at right angles to the vertical shaft and proved more difficult and lengthy. No voiding of cloacal fluid was observed during the nesting.

1126 h Nest site completed.

1127 h Tortoise began to lay eggs. Each egg positioned in the egg chamber using each hind foot alternatively. Ten eggs were laid.

1130 h Egg-laying completed, the tortoise began to refill nest chamber by scooping soil from edge and again using the two hind feet. Once the vertical shaft had been filled, it began to compact the soil by raising itself on three legs and then letting the body fall onto the soil. This procedure appeared to be critical, as the tortoise spent several minutes repeating the process.

1140 h Refilling and compaction completed, the tortoise rested for several minutes. After the rest period it replaced vegetation over the nest site, using the hind feet. Once this procedure had been completed, the nest site was almost unrecognisable.

1145 h The tortoise returned to the lake.

Total time taken to travel to the nest site, dig egg chamber, lay eggs, refill and compact soil and return to the lake, was 1 h and 50 mins. Nesting varied considerably with climatic and soil conditions. Mean temperatures on day of nesting—spring 22.3°C (20.6°C to 24°C) and summer 28°C (25.9°C to 32.1°C).

Ascent to nesting site.—Once the females were some distance from the water's edge they were not easily disturbed and continued in the general direction of the nesting site. Whenever females were handled they would void copious amounts of fluid and return to the lake without nesting. The females did not deviate greatly from the direction in which they were travelling to the nest site. Only during the latter stages of the ascent did the female deviate to look for a suitable nest site. All females took advantage of any thick cover, presumably to avoid attacks by birds.

Distance to nest site.—Distance to nest site varied considerably between the spring and summer nesting periods (Table 3). Moll and Legler (1971) state that distances travelled from water by females of *Pseudemys scripta* are also variable. The greatest distance to a nest site was 105 m which was recorded in the spring nesting period, and the shortest distance to a nest site was 20 m which was recorded in the summer nesting period.

Table 3

Differences in distances to nest site between the spring and summer nesting periods

	Sept.-Nov.	Dec.-Jan
Mean distance to nest sites in metres (No. of nests)*	86·56 ± 10·00 (27)	25·38 ± 2·41 (80)

* p << 0·001, Student's "t" test.

Nest site.—Female tortoises appeared to have no preference for a nest site and generally chose one that was open and free from thick vegetation (Fig. 6).

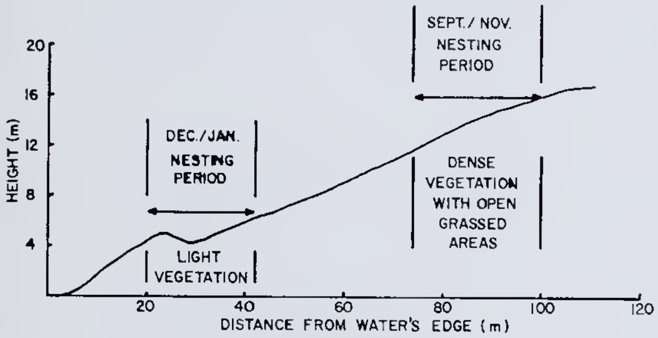

Figure 6.—A typical profile showing distances to nest sites for the two nesting periods.

Neotropical sliders also tend to nest in relatively open areas (Moll and Legler 1971). Females nesting in the summer period generally nested in heavier soils compared with the sandy soils used during the spring nesting period.

Clutch size, egg size and weight

The largest clutch (12 eggs) was recorded in the spring nesting period of 1975, and the smallest clutch (3 eggs) was recorded in the summer nesting period of 1975/1976. Egg size and weight vary within the clutch and between individuals (Tables 4 and 6).

Table 4

Differences in clutch sizes between the two nesting periods

	Sept.-Nov.	Dec.-Jan.
Mean clutch size (No. of nests)*	8·20 ± 1·22 (15)	4·00 ± 0·21 (10)

* p << 0·001, Student's "t" test.

Table 5

Mean temperature (°C) of air and nests between egg-laying and hatching taken over a period of 30 weeks

	Air temperature	Nest temperature	Significance (*)
Minimum	14·85 ± 0·67	20·39 ± 0·74	P < ·001
Maximum	28·18 ± 0·84	27·26 ± 1·00	NS
Difference	13·56 ± 0·44	6·87 ± 0·44	P < ·001

* Student's "t" test for paired samples.
NS—No significant difference.

Eggs taken from the two nesting periods of 1974/1975 and 1975/1976 show very little variation in the time of incubation. In 1974/1975, 216 to 222 days were recorded to hatching, and in 1975/1976, the period was 210 to 220 days. The average temperature in the egg chamber ranged from a minimum of 14°C. to a maximum of 29.8°C. There was a significant difference between the average minimum temperature of the nest and air temperatures (Table 5).

Discussion

The dark and opaque nature of the swamp water has unfortunately precluded any direct observation of *C. oblonga* copulating in the water. Burbidge (1967) states that *C. oblonga* were observed copulating in captivity, and that the copulatory ritual was similar to that of *Pseudemydura umbrina* and that copulation takes place in the water with the male mounting the female from the rear, as does *Pseudemys scripta* (Moll and Legler 1971). In contrast to *Chelonia mydas* (the green sea turtle) studied by Hendrickson (1958) in Sarawak, both female and male *Chelodina oblonga* leave the water and can be found on land, although the percentage of males is well below that of the females. The males do not appear to move during the peak nesting periods (Table 2).

Brattstrom (1965) reports that *Chelonia* are active over a much wider range of body temperatures

Table 6

Animal weights, mean egg size and clutch size of live animals

Animal No.	Animal weight before egg laying (g)	Carapace width (mm)	Carapace length (mm)	Egg weight (g)			Egg length (mm)			Egg width (mm)			Clutch size
				Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	
7372	1 440	224·2	134·2	11·7	11·3	11·5	36·6	35·0	35·7	23·2	22·5	22·9	8
7369	1 250	224·0	127·8	12·0	10·9	11·4	36·7	35·2	32·8	23·4	22·9	23·2	12
7375	1 170	212·8	125·4	10·9	9·9	10·4	33·8	32·2	33·1	23·5	22·6	23·0	10
7378	670	113·0	113·0	6·8	5·8	6·3	31·3	30·0	30·8	18·3	18·0	18·1	6

than terrestrial lizards. Burbidge (1967) cites Lucas (1963) in stating that *Chelodina oblonga* has a preferred temperature of between 16°C and 28°C and that from incidental observations *C. oblonga* is active within the range 13°C to 28°C. During this study the body temperature ranged from 18°C to 31°C (Fig. 3). Tolerance of air temperatures above 25°C is minimal as the animals can only survive a few hours due to desiccation.

Migrations have been reported in a number of species of turtles while nesting, such as *Chelonia mydas* and *Lepidochelys kempi* (Carr 1967), *Batagur baska* (Loch 1950), *Podocnemis expansa* (Roze 1964). Moll and Ledler (1971) state that migratory behaviour has evolved where suitable nesting sites are scarce and where feed is inadequate. Migration could be an important factor for the survival of the species.

During this study no females that were marked during the spring nesting were recaptured during the summer nesting. Professor J. M. Legler (University of Utah) has examined specimens of *C. oblonga* ovaries. Results of his investigations indicate that double nesting could occur (Legler, pers. comm. 1976). Carr (1952) suggests that the Chelonidae and Dermochelyidae do have multiple clutches.

It is suggested that females close to shore prior to nesting are (a) sensing climatic changes, i.e. a rain-bearing depression and/or a falling barometric pressure, (b) absorbing cloacal fluid prior to nesting and (c) absorbing body heat in the shallower warmer water.

Although there is a seasonal difference between the nesting behaviour of *C. longicollis* as described by Vestjens (1969), there appears to be no great difference between the two species in the excavation of the nest site, except for size. The nest size of *Pseudemys scripta* as described by Moll and Legler (1971) is similar in size to that of *C. oblonga*. The egg chamber of *C. longicollis* is smaller than that of *C. oblonga*.

Burbidge (1967) states that *C. oblonga, C. steindachneri* and probably all other Chelidae, possess a pair of bladders opening laterally into the cloaca in addition to the urinary bladder which opens ventrally. Goode and Russell (1968) state that *Chelodina longicollis* and *C. expansa* void copious amounts of cloacal fluid during the excavation of the nest site. *C. expansa* puddles its eggs in the mud produced by the excretion of the cloacal fluid. During this study it was impossible to determine when the cloacal fluid was voided during egg laying as the tail is held tight and close to the body while excavating the egg chamber. Cloacal fluid analysed by Burbidge (1967) shows that it is the same constituency as that of the lake water from which the tortoise is collected.

Some difficulty was experienced in locating females that were nesting, but it is evident from the few samples obtained that larger females lay larger and heavier eggs than smaller females (Table 6). The average clutch size for the summer nesting period was significantly lower than that of the spring nesting period (Table 5). Due possibly to the intense heat during the summer nesting period females moved a much shorter distance than the females moving to nest during the spring nesting period. (Table 3).

Incubation times during this study varied from 210 days to 222 days, compared with 138 days for *C. longicollis*, 342 days for *C. expansa*, and 75 days for *Emydura macquari*. (Goode and Russell 1968). Eggs laid in the spring nesting period hatch in 210 to 222 days and remain underground in an embryonic position until they emerge. Eggs laid in the summer nesting period take as long to incubate but remain in the nest for a shorter period, and young emerging at the same time (mid-August) as hatchlings from the spring nesting period. Reports by amateur observers tend to support the findings of this study that the young emerge about mid-August, with slight variations depending on seasonal conditions.

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